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Seagrasses of the Genus *Halophila* Thouars (Hydrocharitaceae) from Japan

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A taxonomic study of the seagrass genus *Halophila* Thouars concludes that eight distinct taxa, including four new species, occur in Japanese waters. Past literature indicated that the name of *H. ovata* Gaud. is illegitimate, thus a new species name, *H. gaudichaudii* J. Kuo, with a description is provided. *Halophila major* (Zoll.) Miq. has been reinstated to a distinct taxon, with *H. euphlebia* Mak. as a synonym. The other three new species, *H. nipponica* J. Kuo, *H. mikii* J. Kuo, and *H. okinawensis* J. Kuo are endemic to Japan, while *H. gaudichaudii*, *H. ovalis* (R. Br.) Hook. *f.*, *H. major*, *H. minor* (Zoll.) den Hartog and *H. decipiens* Ostenf. are extended from Indo-West Pacific regions to reach their northern distributional boundaries in southern Japan. *Halophila okinawensis* and *H. gaudichaudii* are restricted to Ryukyu Islands and *H. mikii* only occurs in Tanegashima and Yakushima Islands. *Halophila nipponica* is widely distributed in temperate Japan except for Hokkaido Island, while the tropical *H. major* has additional colonies confined to Wakayama Prefecture in Honshu and Tokushima and Kochi Prefectures in Shikoku. Typifications, morphological descriptions, habitat and biological information, illustrations and distribution maps are presented for each taxon. Biogeographical distribution of the Japanese species is discussed in relation to the effect of currents.

Key words: distribution, Hydrocharitaceae, Japanese *Halophila*, seagrasses, taxonomy

The seagrass genus *Halophila* Thouars (1806) has a wide geographic range along the tropical and the warm temperate coastlines, predominantly in the Indo-West Pacific Oceans, and is well known as an extremely eurybiontic genus (den Hartog 1970, Kuo & den Hartog 2001, den Hartog & Kuo 2006). According to den Hartog (1970), *Halophila* had ten species and *H. ovalis* (R. Br.) Hook. *f.* was the only one occurring in Japan. Den Hartog's (1970) *H. ovalis* represented a 'collective species' in which a number of closely allied taxa were united and contained at least eight specific synonyms and five subspecies. Recently, two of these subspecies and one of synonyms have been re-erected to species status as *H. australis* Doty & Stone (Robertson 1984) and *H. hawaiiana* Doty & Stone (Phillips & Meñez 1988), while *H. madagascariensis* Doty & Stone has been recognised as lectotype of the genus (den Hartog & Kuo 2006). Furthermore, since 1970, three more *Halophila* species and a new subspecies of *H. ovalis* have been described. Currently, up to fifteen species and three subspecies of *Halophila* in five sections are included in the latest species list. It is expected that more (new) species will be added when the revision of the genus is completed (Kuo & den Hartog 2001, den Hartog & Kuo 2006).

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Matsumura (1895) reported *Halophila ovalis* from Okinawa Island, which was the first scientific seagrass publication in Japan. Makino (1896) listed five species of seagrasses from Japan including *H. ovalis* from Ryukyu Islands. Furthermore, Ito (1899) found *H. ovalis* from Iriomote Island. Matsumura (1905) recorded *H. ovata* Gaud. (=*H. ovalis*) growing in Miura (Sagami), Noto and the Ryukyu Islands. In addition to *H. ovalis*, which is found in Sagami (Misaki), Sanuki (Kozai) and Noto (Uchiura), Makino (1912) described a new species *H. euphlebia* Mak. from Shikoku, and commented that *H. ovata* does not exist in Japan. Miki (1934a) discussed the two species, *H. ovalis* and *H. euphlebia*, in the Section *Halophila* in Japan and suggested that there were three distinct geographical and morphological forms of *H. ovalis*: a. Northern, b. Southern, and c. Intermediate forms. Miki (1934a) originally treated *H. euphlebia* as a Southern form of *H. ovalis*, but later (Miki 1934b) recognized that only *H. ovalis*, without different morphological and geographical forms, occurred in Japan. The "New Illustrated Flora of Japan" recognized two species (*H. ovalis* and *H. euphlebia*) (Makino 1961, Maekawa *et al.* 1988), while all other Japanese floristic treatments followed Miki's (1934b) classification (*e.g.*, Ohwi & Kitagawa 1983, Yamashita 1991, Kitamura *et al.* 1998). Den Hartog (1970) probably also followed Miki's (1934b) since he treated *H. euphlebia* as a synonym of *H. ovalis*. Kuo *et al.* (1995) were the first to report that *H. decipiens* Ostenf. occurred in Okinawa Island. Aioi & Nakaoka (2003) listed only two *Halophila* species, *H. ovalis* and *H. decipiens*, in Japan.

Probably based on a molecular study by Waycott *et al.* (2002), Green & Short (2003) listed only ten *Halophila* species in the world and proposed that several established *Halophila* species should be treated as 'conspecific with *H. ovalis*'; a similar concept to the 'collective species of *H. ovalis*' by den Hartog (1970). Taxonomy of *H. ovalis*, as defined by den Hartog (1970), has been a problem for accurately identifying the species of *Halophila* from Japan and also from elsewhere in the world, because the species had a lamina that ranged from 10-40 (-70) mm long and 5-20 mm wide with cross veins of 10-25 pairs and contained about eight synonyms including *H. euphlebia* and *H. major* (Zoll.) Miq. On the other hand, Green & Short's (2003) treatment of *H. ovalis* included already established species such as *H. ovata*, *H. minor*, *H. hawaiiana* and *H. johnsonii* Eiseman, but these authors did not provide a description of so called *H. ovalis* nor did they carry out a taxonomic study of *Halophila*. Their *H. ovalis* probably will have a much broader morphological range than that of den Hartog's. Recently, Uchimura *et al.* (2005) proposed six *Halophila* species from Japan: *H. ovalis*, *H. decipiens*, *H. australis*, and *H. minor* and two unnamed species in their presentation at the 29th Annual Meeting of the Japanese Society of Phycology. These authors did not undertake a typification and nomenclatural study of the species concerned, thus, their work contained serious taxonomic problems and incorrect scientific names were applied.

This work is based on a comprehensive review of the literature on *Halophila* and a thorough examination of the relevant specimens, including types, which are housed in the principle herbaria in the world, as well as the freshly collected material from various geographic localities and a wide range of habitat. It concludes that there are eight distinct taxa of *Halophila* including four new species of *Halophila* occurring in Japan.

Materials and Methods

Herbarium specimens

More than three thousands specimens of *Halophila*

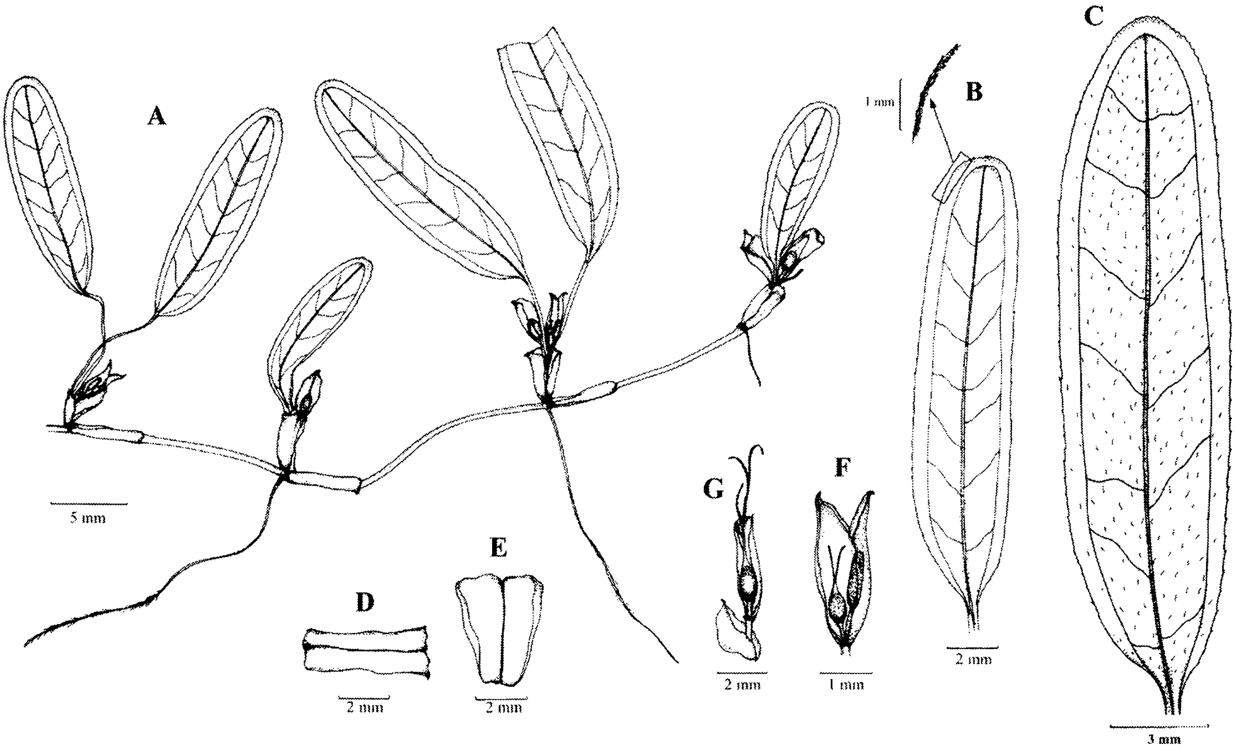

FIG. 1. Drawings of *Halophila decipiens* Ostenf. A, flowering plant; B, a lamina with an enlarged margin; C, lamina with hairs; D, rhizome scale (opened); E, petiole scale (opened); F, overlapping spathal bracts coverings both male and female flowers; G, female flower with extended styles.

from 65 herbaria were studied. In general, there were very few Japanese specimens in the foreign herbaria, most of them from the Ryukyu Islands. Overseas herbaria that had Japanese *Halophila* specimens included C, GU, K, L, LD, NY, US. The most important Japanese herbaria for *Halophila* are KYO, MAK, TI and TNS. Other minor Japanese herbaria included OSA, SAP, TSU, Faculty of Fisheries Herbarium, Fishery Department Herbarium, Kyushu University, Kagoshima (KYU); and the Kagoshima Fishery Experiment Station, Kagoshima (KF). Among these examined specimens, only types and those collected from Japan were discussed in this paper.

Freshly collected specimens

More than 120 additional fresh collections were made around Japan over the last twenty years with the help of numerous Japanese colleagues. They cover the full geographical and habitat range of the *Halophila* species and are stored at the Centre for Microscopy and Microanalysis, the University of Western Australia (CMM).

Macrography, morphological studies and measurements

More than 90% of these herbarium and fresh collections were macrographed and each specimen was examined under a dissecting microscope. Root length, rhizome diameter, internode, petiole, and lamina length and width of each specimen were measured; the number and nature of cross veins were also recorded. In addition, the distance from lamina intramarginal veins to lamina margin and the distance between two adjacent cross veins were also measured for numerous specimens. It should be noted that to prevent measuring 'immature' samples, all measurements were taken from leaves at least at the second node from the developing rhizome apex. When available, reproductive structure was measured and noted. All original drawings and photographic negatives are kept at CMM.

Results

Halophila Thouars in Madag. 2: 2 (1806)
Type: *Halophila madagascariensis* Doty & Stone [P-lect, see Doty & Stone (1967)].

Monoecious or dioecious. Annual or perennial marine plants with creeping, monopodial rhizomes, rooting and with erect lateral shoots at the nodes. Scales 2, one covering rhizome, another covering petiole base. Leaves in pairs, arising from an extremely short lateral shoot. Lamina variable in shape and size, usually dorsi-ventrally flattened; surface glabrous or pilose; margins entire or serrulate; longitudinal veins 3, a midrib and 2 intramarginal veins that are connected by ascending or perpendicular cross-veins. Inflorescence sessile, spathal

Key to species of the Japanese *Halophila*

1a. Lamina margins serrulate, surface usually with hairs; lateral shoots distinct; monoecious ………… *H. decipiens*
1b. Lamina margins entire; surface glabrous; lateral shoots indistinct; dioecious ………… 2
  2a. Distance between intramarginal veins and lamina margin distinctly narrow, ratio between distance from intramarginal veins and to lamina margin and half of lamina width >10 ………… 3
  2b. Distance between intramarginal veins and lamina margin wide, ratio between distance from intramarginal veins and to lamina margin and half of lamina width <9.5 ………… 6
    3a. Lamina less than 12 mm long, narrower than 4.5 mm wide; cross veins 7-12, rarely or no branched, at each side of midrib ………… *H. minor*
    3b. Lamina longer than 12 mm, wider than 6.5 mm; cross veins 12-22, often branched at each side of midrib ………… 4
      4a. Lamina with cross veins (16-) 18-22; 1/2 lamina width : distance between intramarginal veins and lamina margin ratio 1 : 20-25 ………… *H. major*
      4b. Lamina with cross veins 12-16 (-18); 1/2 lamina width : distance between intramarginal veins and lamina margin ratio 1 : 12-16………… 5
        5a. Lamina ovate to elliptic, not spatulate; lamina L:W ratio 1.6-2.0; cross veins 12-16 (-18) (widely distributed in subtropical regions) ………… *H. ovalis*
        5b. Lamina distinctly spatulate; lamina L:W ratio 3-4; cross veins 14-17 (endemic to Tanegashima-Yakushima Islands) ………… *H. mikii*
          6a. Lamina 15-30 mm long, 5-13 mm wide; cross veins (6-) 7-9 (-10) (endemic to Honshu, Kyushu and Shikoku) ………… *H. nipponica*
          6b. Lamina less than 16 mm long, less than 4.5 mm wide; cross veins less than 8 (distributed in subtropical regions) ………… 7
            7a. Lamina distinctly linear to spatulate, base narrowed; lamina L:W ratio (2.5-) 3.5-4 (-7); cross veins (5-) 6-7 ………… *H. okinawensis*
            7b. Lamina usually ovate to obovate, base rounded; lamina L:W ratio (1.6-) 2-2.4 (-7); cross veins (3-) 4-8 ………… *H. gaudichaudii*

bracts in pairs covering either one flower or two flowers of different sex. Male flowers with peduncle extending at anthesis, tepals 3, stamens 3; anthers sessile, pollen grains united into moniliform chains. Female flowers with 1 ovary extending to hypanthium, styles 3, filiform, undivided. Fruit ovoid or globose, pericarp membranous and decays to release seed. Seeds variable number, ovoid or globose, testa mostly reticulated.

Notes: Halophila is widely distributed in all tropical seas, extending also into subtropical and warm-temperate waters. Five Sections have been recognized but only Section *Halophila* occurs in Japanese waters (den Hartog 1970, Kuo & den Hartog 2001, den Hartog & Kuo 2006). The description above applies only to the Japanese species.

Description of Japanese *Halophila* species

Halophila decipiens Ostenf., Bot. Tidsskr. 24: 260, with fig. (1902); Kuo *et al.*, Aquat. Bot. 51:329-334, with figs (1995), (Figs. 1, 9). Type: Gulf of Thailand, off Koh Kahdat, on coral sand, 5 fathoms deep, February 1900, *J. Schmidt 540* (C-holo; L-iso).

Monoecious. Annual. Rhizome slender, internodes (10-) 15-25 (-35) mm long, 0.5-0.8 mm in diameter, root to 50 mm long. Lateral shoot 3-5 mm long, 1 mm wide. Scales 2, transparent, obovate, apex mucronate, base subtruncate, keeled, 3-5 × 2-3 mm, margins entire, outside hairy. Leaves petiolate. Petiole slender, transparent, 5-10 mm long. Lamina pale green, elliptic, to 20 mm long, 4-6 mm wide, L:W ratio ca. 2.5-3; apex obtuse; base attenuate to cuneate; margins finely serrulate; surfaces with dense stiff unicellular hairs; distance between intramarginal veins and lamina margin 0.25-3 mm wide; 1/2 lamina width: distance between intramarginal veins and lamina margin ratio ca. 1:2-3; cross veins 6-9, unbranched, ascending, joining the intra-marginal veins; distance between adjacent cross veins 1.5-2 mm wide. Spathe with two overlapping bracts; bracts ovate, transparent, 3-4 × 2-3 mm, apex acuminate to mucronate, keeled, outside sparse hairs; keels and margins finely serrulate, enclosing one male and one female flower. (Male flower) tepals oblong to elliptic, convex, 1.5-2 mm long, pedicel rather thick, to 5 mm long at anthesis, anthers ca. 1 mm long. (Female flower) ovary ovoid, ca 1-1.5 × 1 mm; hypanthium 1.5 mm long; styles 4-6 mm long. Fruit broadly ellipsoid to ovoid, yellowish to brownish, 5 × 4 mm, with persistent hypanthium. Seeds, 20-30, ovoid, cream white to pale yellow, 0.55 × 0.5 mm; ends bluntly beaked; testa reticulate.

Distribution and habitat: Halophila decipiens is the most widely distributed seagrass species in the world. In Japanese waters it is only known to occur in several localities in Iriomote Island and Okinawa Island and the latter is the northern distributional limit of the species. In Japanese waters, *H. decipiens* only grows sparsely in deep clear water from about 5.5 m down to 38 m on coral sand as mono-specific patches or occasionally mixed with *H. okinawensis* and *H. gaudichaudii.*

Biology: *Halophila decipiens* is the only monoecious *Halophila* in Japan and is an annual species. The seedling appears in February to March; flowers and seeds occur in May to July and plants disappears from the sites by September to November (see Kuo *et al.* 1995).

Affinity: This is the easiest species to be distinguished from other Japanese *Halophila* by having lamina with serrulated margins and hairy surfaces. It is also the only monoecious *Halophila* species in Japan.

Selected specimens examined: JAPAN: **Okinawa Pref.**: Iriomote Isl., Amitori Bay, 20-30 m, Dec 1993, *H. Yokochi* (CMM); *loc. cit.*, 38 m, 7 June 1999, *H. Yokochi & Z. Kanamoto* (CMM). Okinawa Isl., Nakagusuku Bay, 18 m, 23 June 1994, *T. Toma & Z. Kanamoto* (CMM); Kin Bay, 19 m, with *H. okinawensis* and *H. gaudichaudii*, 29 June 1998, *Z. Kanamoto* (CMM); Sesoko Island, 20 m, sparse growth, 7 July 1994, *S. Nakamura* (CMM); *loc.*

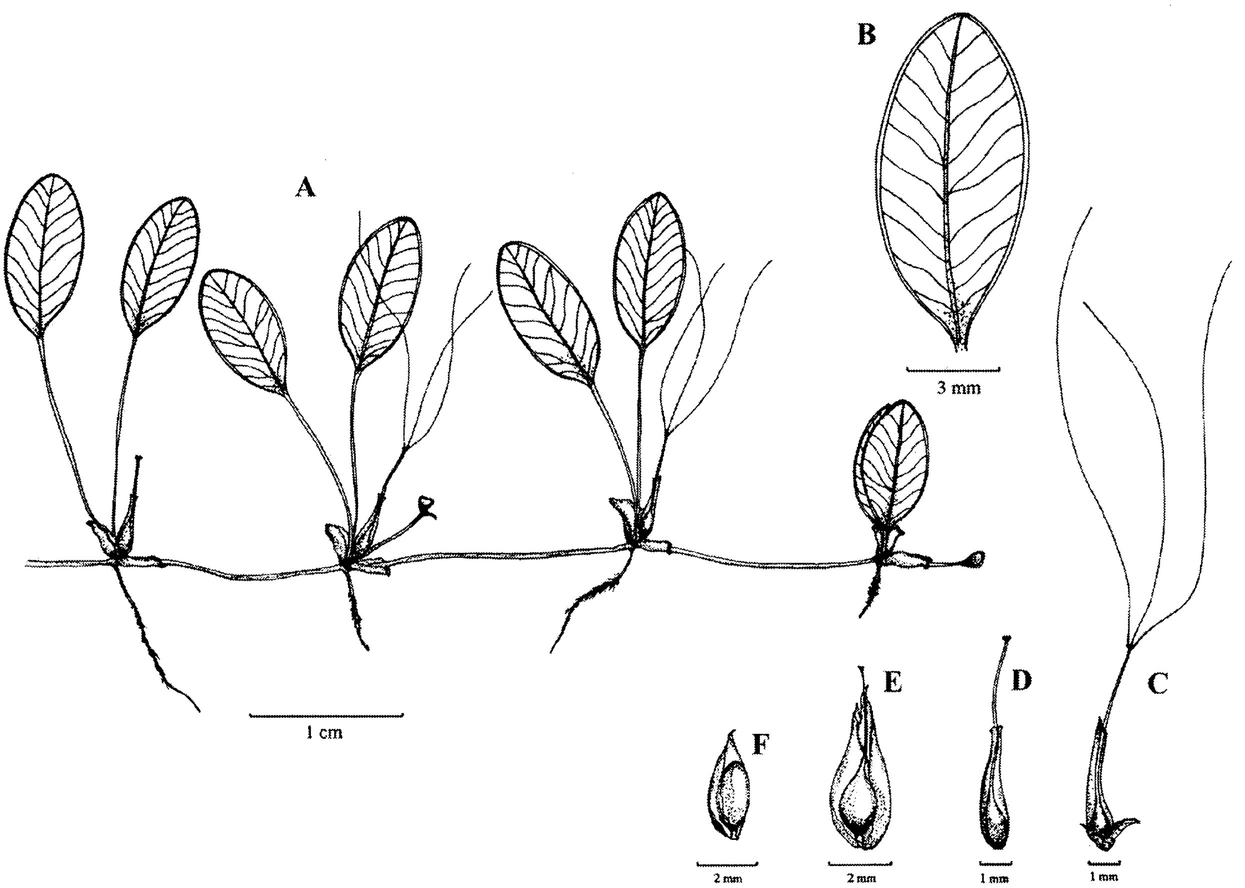

FIG. 2. Drawings of *Halophila minor* (Zoll.) den Hartog. A, female flowering plant; B, lamina; C, female flower with 3 elongated styles attached; D, female flower with styles detached; E, maturing fruit; F, tepals.

cit., 24 m, sandy bottom, with *H. okinawensis* and *H. gaudichaudii*, 26 Aug 1994, *M. Nishihira* (CMM); Ikei Jima, near light house, 17 m, 4 May 2001, *S. Tanahara* (private collection); Awase, 6.5 m, sand, with *H. okinawensis*, 9 May 2003, *S. Tanahara* (private collection); same but 5.5 m, with *H. minor*, 15 June 2003.

Halophila minor (Zoll.) den Hartog, Fl. Males. I, 5: 410, f. 17b (1957), (Figs. 2, 10)

Lemnopsis minor Zoll., in Zoll. Syst. Verz. 1: 75 (1854); *Halophila lemnopsis* Miq., Fl. Ind. Bat. 3: 230 (1855), based on *Lemnopsis minor* Zoll., *nom. illeg. Halophila ovalis* var. *minor* (Zoll.) Asche., Linnaea 35: 173 (1868). Type: Indonesia, Lesser Sunda Islands, Flores, near Bari, 12 July 1847, *H. Zollinger 3334* (BM-holo; P, L-iso).

Dioecious. Perennial. Rhizome slender, fleshy, transparent, internodes to 30 mm long, 0.5 mm diameter. Lateral shoots invisible. Leaves petiolate. Scales 2, surface glabrous, margins entire, one scale embracing the base of the petioles, ovate to oblong, apex retuse, base subtrucate, 3 × 1.5-2 mm, convolute, transparent, the other embracing the rhizome, oblong, apex retuse, base truncate, 3-4 × 1-1.5 mm, convolute, hyaline. Petioles fleshy, transparent, 5-10 mm long. Lamina bright green, ovate, to 10 mm long, 4-5 mm wide, L:W ratio 1.8-2.2; apex acute or acuminate; base cuneate to attenuate, symmetrical; margin entire; surface glabrous; distance between intramarginal veins and lamina margin 0.15-0.4 mm wide; 1/2 lamina width: distance between intramarginal veins and lamina margin ratio 1:11.5-16.3; cross veins 7-12, rarely branched; distance between adjacent cross veins 0.65-0.85 mm wide. (Male flower) two overlapped spathal bracts glabrous, 2.5-4 × 1-1.5 mm; tepals 2-3.5

mm long; anthers three, fused, oblong, 2.5-3 × 1.2-1.5 mm. (Female flower) spathal bracts glabrous, 3.5-4 mm long; ovary elliptic to ovoid to elliptical, white; 1-1.5 × 0.5 mm; hypanthium 4-6 mm long; styles 8-20 mm long. Fruit ovoid, covered by keeled yellowish to brownish spathes; 2.5 × 2-3.5 mm. Seeds 15-30, ovoid, 0.5 mm diameter, ends bluntly beaked; testa reticulate.

Distribution and habitat: The species is disjunctively distributed in the tropical Western Pacific Ocean and southern subtropical Japan northward to Amami-oshima Island. *Halophila minor* normally grows on coral sand or muddy sand together with *H. ovalis* or *H. major* and with other tropical seagrasses in shallow water. It also extends into deeper water down to 7 m where it forms sparse patches or with other species such as *H. okinawensis* and *Halodule pinifolia*.

Biology: Flowering is from June to September and fruiting is in August and September.

Nomenclature notes: *Lemnopsis minor* was transferred to the genus *Halophila* by Miquel (1855), but under the name of *H. lemnopsis*. Ascherson (1868) recognized the species *L. minor* as one of three 'varieties' along with var. *major* and var. *ovata* of *H. ovalis*. However, Ascherson in his later publications (*e.g.*, Ascherson 1888, 1906) did not mention this taxon presumably because he considered this taxon to be *H. ovalis*. Den Hartog (1957) transferred the species *L. minor* from the genus *Lemnopsis* to *Halophila* and considered it to be a distinct species with *H. ovata* (now *H. gaudichaudii*) as a synonym. However, den Hartog (1970) reversed the order and placed *H. minor* as a synonym of *H. ovata* which he recognized as having priority. Sachet & Fosberg (1973) followed den Hartog's concept and treated *H. minor* and *H. ovata* as conspecific, but concluded that the name *H. ovata* (Gaudichaud 1826, 1827, 1829) was illegitimate (see more under *H. gaudichaudii*). Kuo (2000) clarified the confusion and recognized *H. minor* and *H. ovata* as two distinct species. Furthermore, Sachet & Fosberg (1973) retreated *H. madagascariensis* as a synonym of *H. minor* instead of *H. ovalis* as described by den Hartog (1970). Currently, *H. madagascariensis* has been restored as the lectotype of the genus *Halophila* (den Hartog & Kuo 2006).

Affinity: Because the size of *Halophila minor* is very similar to that of *H. ovata* (now *H. gaudichaudii*) they have been considered to be conspecific under either species names (*e.g.*, den Hartog 1957, 1970, Sachet & Fosberg 1973). However, characters such as the distance between the lamina margin and the intramarginal veins and between adjacent cross veins, and the number of cross veins all clearly demonstrate that they are two distinct species (see Kuo 2000). Furthermore, the size of the plants and lamina as well as the number of cross veins can also easily separate *H. minor* from *H. ovalis* and its allies.

Selected specimens examined: JAPAN: **Okinawa Pref.**: Ryukyu (Loo-Choo) Isl., no locality, USA Pacific Expedition 1853-56, *C. Wright 327* (US71272). Iriomote Isl., no locality, 7 Aug 1919, *S. Kawagoe* (US2071414); Ohara, sand substrate, 23 Apr 1958, *T. Amano 7319* (TNS116402; US2156298); Shirahama, sandy at ebb-tide, 15 Mar 1968, *T. Yamashita* (TI); Taketomi Cho, Hoshidate, 27 Mar 1979, *T. Kubo* (TI); Amitori Bay, 0 m, Dec 1993, *H. Yokochi* (CMM); *loc. cit.*, 1 m, 7 June 1999, *Z. Kanamoto & J. Kuo* (CMM). Ishigaki Isl., Kabira Bay, 0.5 m, 14 Nov 1993, *K. Shimamura* (CMM); Nagura Bay, 0.5 m, 14 Nov 1993, *K. Shimamura* (CMM); *loc. cit.*, 1 m, 4 June 1999, *Z. Kanamoto & J. Kuo* (CMM). Okinawa Isl., Itoman, on coral reef, 10 June 1955, *S. Hatsusima 18133* (TI, US2243444); Yagachi Island, 0 m, 24 June 1966, *E. H. Walker 8421* (L63161254; US2619565); Shinzato, MLLW, 26 Jan 1990, *R. T. Tsuda 90-47* (GU); Henoko, 0.5-1 m, (MLLW), 9 Mar 1990, *R. T. Tsuda 90-74* (GU); S of Cape Bise-zaki, MLLW, 20 Jan 1990, *R. T. Tsuda 90-36* (GU). Amami-oshima Isl., Atetsu, 8 m, white sand; Doren, 3 m, on coral sand, with *Halophila ovalis*, *Halodule* spp.; Ankyaba, 10 m, on white sand, adjacent to corals, 13 June 1999, *J. Kuo & Z. Kanamoto* (CMM); Maehada, 2-3 m, with *H. ovalis*, *Halodule* spp., 14 June 1999, *Z. Kanamoto & J. Kuo* (CMM); Kasari, with *H. ovalis*, 30 Oct 1967, collector unknown (KYU); Sumiyo, June 1991, collector unknown

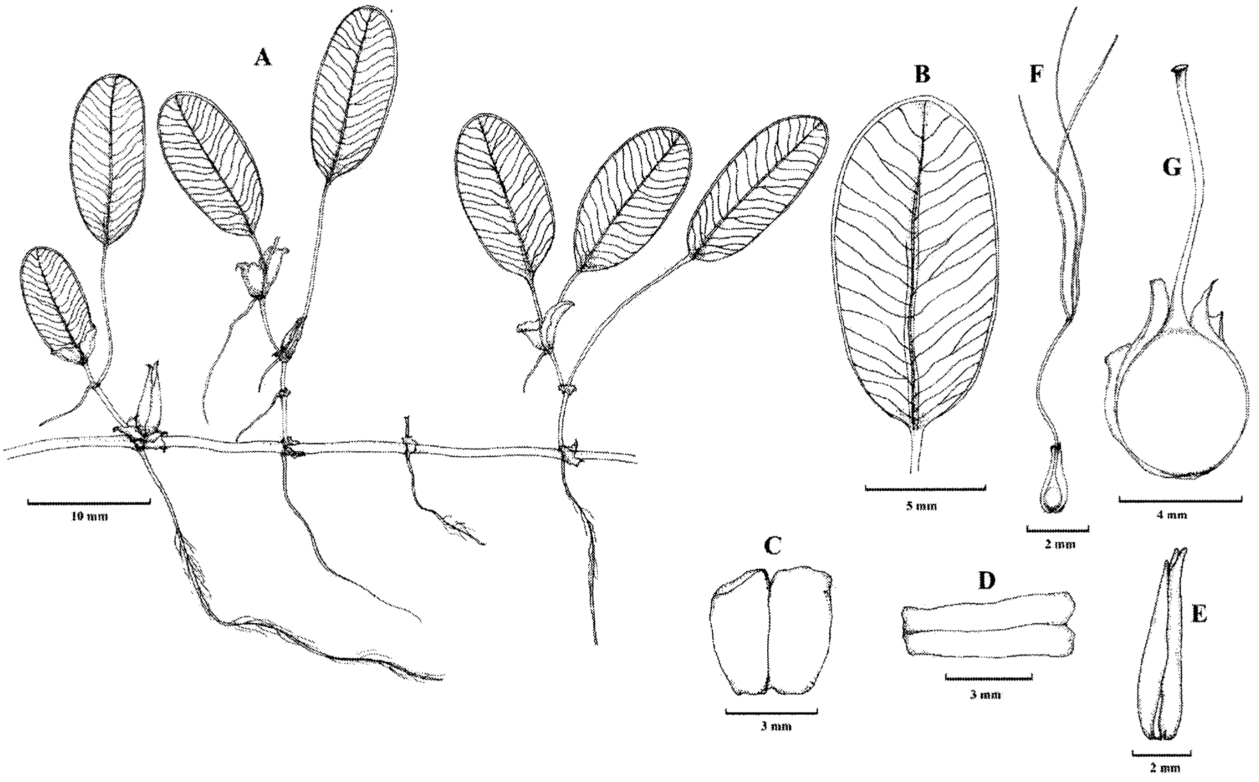

FIG. 3. Drawings of *Halophila major* (Zoll.) Miq. A, female flowering plant; B, lamina; C, petiole scale (opened); D, rhizome scale (opened); E, spathal bracts; F, female flower with 3 elongated styles; G, maturing fruit with a persisted hypanthium.

(KF).

Halophila major (Zoll.) Miq., Fl. Ind. Bat. 3: 230 (1855), (Figs. 3, 11)

Lemnopsis major Zoll., Syst. Verz. 1: 75 (1854); *Halophila ovalis var. major* (Zoll.) Asche., Linnaea 35: 174 (1868); *Halophila euphlebia Mak.*, Bot. Mag. Tokyo 26: 208, fig. XV(1912). Lectotype: Indonesia, Sumbawa, Kambing in the Bay of Bima, October 1847, *H. Zollinger* 3430 (P, lectotype here designated; BO; L59 90515349; L60 905170100; U; Z-iso).

Dioecious. Perennial. Rhizomes slender to robust, fleshy, transparent, internodes (20-) 25-40 (-50) mm long, 1.5-2 mm diameter; roots up to 50 mm long, 1.5 mm diameter. Lateral shoots invisible. Scales 2, glabrous, margins entire, petiole scale 3.5-4.5 × 1.5-2 mm, rhizome scale 4-5.5 × 1.5-2.5 mm. Leaves petiolate. Petioles fleshy, purple to red, (10-) 15-30 (-35) mm long. Lamina bright to dark green, ovata, oblong to elliptic, (13-) 15-25 (-30) mm long, (7-) 9-11 (-13) mm wide, L:W ratio 1.4 - 3 : 1; apex acute or acuminate; base cuneate to attenuate, symmetrical; margins entire; surface glabrous; distance from intramarginal veins to lamina margin 0.16-0.5 mm wide; 1/2 lamina width : distance between intramarginal veins and lamina margin ratio 1 : 20-25; cross-veins distinct, (16-) 18-22, often branched (up to 3 branches), distance between adjacent cross veins 0.7-1.25 mm wide. (Male flowers) spathal bracts 5-6 mm long; tepals 3-4 mm long; anthers, 2.5-3 × 1.2-1.5 mm. (Female flowers) spathal bracts 5.5-6 mm long; ovary ovoid, white, 1.5-2 × 1.5 mm; hypanthium 10-13 mm long; styles 25-40 mm long.

Distribution and habitat: *Halophila major* has two distinct populations in Japanese water. The southern population occurs to the south of Amami-oshima Island, which is widely distributed in the Caroline Islands Group in the Micronesia and West Pacific regions including the Philippines, Thailand, Malaysia, Singapore, Indonesia and Viet Nam. While the northern isolated population (temperate) is restricted to Kii Channel (Tokushima and Kochi Prefectures in Shikoku and Wakayama Prefecture in Honshu). The subtropical *H. major* occurs as small patches or mixed with *H. ovalis* and/or *H. minor* as well as with other tropical seagrasses such as *Halodule* spp., *Cymodocea* spp., *Syringodium isoetifolium* (Aschers.) Dandy or *Thalassia hemprichii* (Ehrenb.) Aschers. in the shallow water of coral sands. On the other hand, the temperate population has been found to form rather large meadows (up to 20 m^2) from 2-7 m in mud to muddy sand substratum in sheltered bays. It often co-exists with other temperate seagrass species, particularly *H. nipponica* and *Zostera japonica* Aschers. & Graebn. At the Kochi Prefecture it grows with *Z. marina* L. and *Z. japonica* in a large meadow about 5 m deep, and with *H. nipponica* patches (1-2 m^2) at 7 m.

Biology: Flowering is from June to September and fruiting is in August and September.

Nomenclature notes: The type material of *Lemnopsis major* (*Zollinger 3430*) has been found in several herbaria, and that at P has been selected as lectotype and those at other herbaria including BO, L, U, and Z as isotypes. Miquel (1855) transferred *L. major* from the genus *Lemnopsis* to the genus *Halophila*. Ascherson (1868, 1882) originally recognized this taxon as var. *major* of *H. ovalis*, but this was not mentioned in his other publications (*e.g.*, Ascherson 1888, 1906). Makino (1912) described *H. euphlebia* based on the specimen collected from Shikoku by Juro Nikai *1613* (holo. at TI, see also Tanaka 2005). Miki (1934b) considered *H. euphlebia* as a synonym of *H. ovalis* and den Hartog (1970) listed both *H. major* and *H. euphlebia* Mak. as synonyms of *H. ovalis*. On the other hand, Makino (1961) and Maekawa *et al.* (1988) treated *H. euphlebia* as a distinct species. After examining global type materials of *H. major* and other related specimens, it is concluded that reinstating taxon status to *H. major* is warranted and *H. euphlebia* is recommended to be a synonym of *H. major*.

Affinity: Morphological characters of *Halophila major* are similar to those of *H. ovalis*, both species normally have a distinct ovate to elliptic lamina and branching cross veins. However, *H. major* usually has a larger lamina with (16-) 18-22 cross veins and represents the ratio of 20-25: 1 for the distance between the intramarginal veins and lamina margin : half of lamina width, while *H. ovalis* has a lamina with 12-16 (-18) cross veins and a ratio of 10 - 16 : 1. Although these two species may occur together in tropical Indo-West Pacific regions, *H. major* has a narrower distribution range than *H. ovalis*.

Selected specimens examined: TAIWAN: Puratasu Isl. (Peng-Hu Is.), June 1908, *T. Kawakami* (TI, paratype of *H. euphlebia* by Tanaka 2005). JAPAN: **Okinawa Pref.**: Luchu Isl., Sea of Yayeyama Archipelago, 12 Aug 1894, *T. Ito 1455* (K). Iriomote Isl., Shirahama, 6 Aug 1968, *T. Yamashita* (TI). Ishigaki Isl., Oohama, 30 Oct 1969, *T. Yamashita* (TI). Okinawa Isl., Onoshima, Oct 1901, *K. Ando* (MAK226967); no exact locality, *K. Ando* (MAK226968); Awase, 5 m, 27 Sept 2003, *S. Tanahara* (private collection). **Kagoshima Pref.**: Amami-oshima Isl., Aug 1911, collector unknown (MAK226966). **Tokushima Pref.**: Kaifu gun, Shishikui Mura (type locality of *H. euphlebia* Mak.), 7 m, with *Zostera marina*, 10 June 1998, *Z. Kanamoto & I. Fukui* (CMM). **Kochi Pref.**: Toyo Town, Kannoura, 6-7 m, with *Z. japonica* and *H. nipponica*, 9 June 1998, *Z. Kanamoto* (CMM). **Wakayama Pref.**: Tanabe, Shirahama, Aug 1902, *K. Minagata* (MAK196340); Tanabe Bay, 26 Sept 1924, *K. Matsushima* (TNS37494); Tanabe Bay, Hatakejima, Sept-Oct 1924, *T. Nakajima* (TI, SAP, KYO); *loc. cit.*, with *H. nipponica*, 1924, *T. Makino* (MAK226960); *loc. cit.*, no date, *K. Morimoto* (MAK226962); Tanabe Bay, 26 Sept 1926, *U. Nuizo* (KYO); Tanabe, Kashima, 6 Aug 1963; off Seto MBL, 0.5 to 1 m, with *H. nipponica*, 21-23 Aug 2003, *T. Kato* (CMM); Kushimoto, 3 m, with *Z. japonica*, 22 Sept 1995, *I. Fukuda* (CMM); *loc. cit.*, but 1 Aug 1997, *I. Fukuda* (CMM); but 3 Sept 1997, *I. Fukuda & Z. Kanamoto* (CMM); with *Z. japonica*, 9 June 1998, *J. Kuo, Z. Kanamoto & I. Fukuda* (CMM); 15 July 1998, *I.*

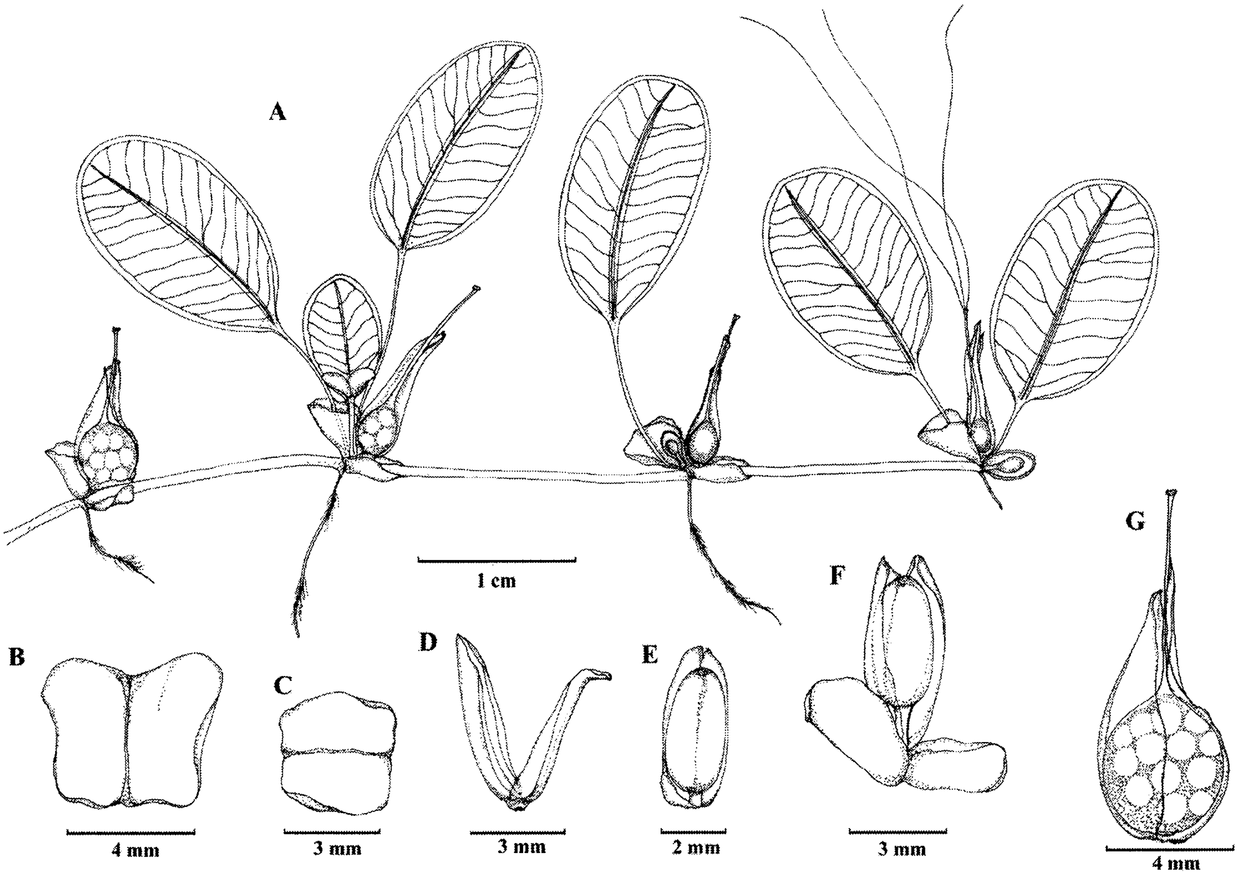

FIG. 4. Drawings of *Halophila ovalis* (R. Br.) Hook. *f.* A, female flowering plant; B, petiole scale (opened); C, rhizome scale (opened); D, spathal bracts; E, tepals with a short pedicel; F, tepals with slightly extended pedicel; G, maturing fruits with a persisted hypanthium.

Fukuda (CMM); June 1999, *Z. Kanamoto & I. Fukuda* (CMM).

Halophila ovalis (R. Br.) Hook. f., Fl. Tasman. 2: 45 (1858), (Figs. 4, 12)

Caulinia ovalis R. Brown, Prod. Fl. Nov. Holl. 1: 339 (1810); *Halophila ovata* Gaud., Bot. Voy. Uranie 65 (1826), Pl. 40 (1827), 429-430 (1829) *nom. illeg.*, based on *C. ovalis*; *H. ovalis* var. *ovata* Aschers., Linnaea 35: 173 (1868) *non. illeg.*, based on *H. ovalis*. Type: Australia, Queensland, the Strait south of Townshend Island, Shoalwater Bay, 24 September 1802, *Robert Brown 5816* (the number was added by Bennett) (BM-holo; K-iso).

Dioecious. Perennial. Rhizomes internodes to (15-) 25-40 mm long, 0.8-1 mm diameter. Scales 2, glabrous, margins entire, petiole scale 4 × 1.5-2 mm, rhizome scale 3.5-4 × 1.5-2 mm. Lateral shoots invisible. Leaves petiolate. Petioles fleshy, purple to red, (5-) 10-25 mm long. Lamina bright green, ovate, elliptic, (10-) 12-18 mm long, 4-8 (-10) mm wide, L:W ratio (1.3-) 1.6-2.0 : 1; apex acute or acuminate; base cuneate to attenuate, symmetrical; margin entire; surface glabrous; distance between intramarginal veins and lamina margin 0.25-0.4 mm wide; 1/2 lamina width : distance between intramarginal veins and lamina margin ratio 1 : 10-16; cross veins 12-16 (-18), often branched, distance between adjacent cross veins 0.8-1.1 mm wide. (Male flower) spathal bracts 3-4 mm; tepals 2.5-3.5 mm long; Pedicel to 20 mm long at anthesis; anthers 2-2.5 mm long. (Female flower) spathal bracts 3.5-4 mm long; ovary ovoid, white, 1-1.5

× 0.5 mm; hypanthium 4-6 mm long; styles 8-30 mm long. Fruit ovoid, covered by keeled yellowish to brownish spathes, 2.5 × 2 mm. Seeds 15-30, ovoid, ca. 1 mm diametre, ends bluntly beaked; testa reticulate.

Distribution and habitat: *Halophila ovalis* is widely distributed in tropical and subtropical Indo-West Pacific regions and extends, in southern Japan, to Amami-oshima Island. This species occurs from intertidal at low tide to about 15 m deep on coral or mud sand, commonly co-existing with other subtropical species including *H. minor* and/or *H. major*. The species also grows adjacent to a submarine hot spring with high sulphide content (5700-8400 μg S g^{-1} DW) and high temperature (28.6°C) at Taketomi Island (see Kuo *et al.* 2001).

Biology: Flowering is in June to September and fruiting is in August and September.

Nomenclature notes: Although den Hartog (1970) indicated "the exact locality" as unknown for Brown's type collection, Stearn (in R. Brown's facsimile edition of the '*Prodromus*' 1960) located the type locality in Brown's note as "Station 23" which corresponded to the strait, south of Townshend Island, Shoalwater Bay, Queensland. J. D. Hooker (1858) transferred the species from the genus *Caulinia* to the genus *Halophila*. Ascherson (1868) recognized three entities in *H. ovalis*: *H. ovata*, *H. minor* and *H. major*. However, in his subsequent publications he only mentioned *H. ovalis* and by 1906 Ascherson's *H. ovalis* contained several synonyms including *H. major*, *H. minor*, and *H. ovata*. Den Hartog (1957) recognized *H. minor* (=*H. ovata*) as a distinct species and separated it from *H. ovalis* which included *H. major*. Den Hartog (1970) considered that *H. ovalis* represented a 'collective species' which contained *H. major*, *H. euphlebia* and *H. madagascariensis* as synonyms and four subspecies: sspp. *hawaiiana*, *bullosa*, *australis* and *linearis*. *Halophila ovalis* had been confused with *H. ovata* (now as *H. gaudichaudii*) or treated as the same species by some early Japanese botanists (Matsumura 1885, 1905; Makino 1886; Ito 1895). However, Makino (1912) considered that *H. ovata* is not present in Japanese waters. Most modern Japanese taxonomists considered that only *H. ovalis* occurred in Japan and treated *H. euphlebia* as a synonym of *H. ovalis*.

Affinity: *Halophila ovalis* commonly occurs in southern subtropical Japan, sometimes co-existing with *H. major* and/or with *H. minor*. The shape of the lamina of these three species is similar, each having ovate to elliptic lamina of different sizes. The most effective characteristics to distinguish these species are the number and branching of cross veins, and a ratio for the distance between intramarginal veins and the lamina margin : half of lamina width. The Japanese *H. ovalis* has 12-16 (-18) cross veins, often branching and a ratio of 10-16; the Japanese *H. major* usually has (16-) 18-22 branching cross veins and a ratio of 20-25 while *H. minor* has 7-10 (-12) no or rarely branched cross veins and a ratio of 11.5-16.3.

Selected specimens examined: JAPAN: **Okinawa Pref.**: Ryukyu Isl., (Loo-Choo Is.), in pools, *C. Wright1853-56* (NY). Sea of Yaeyama Archipelago, 12 Aug 1894, *T. Ito 1455* (K). Iriomote Isl., Shirahama, 29 July 1968, *T. Yamashita* (TI); Amitori Bay, 0.5 m, Dec. 1993, *H. Yokochi* (CMM); *loc. cit.*, 1 m, June 1998, 1-2 m, with *H. minor*, 7 June 1999, *J. Kuo & Z. Kanamoto* (CMM); *loc. cit.*, but ca 500 m from Udara River mouth, with *H. minor* and other tropical seagrasses, 7 June1999, *J. Kuo & Z. Kanamoto* (CMM); Sakiyama Bay, 1-4 m, with *H. minor* and other tropical seagrasses, 8 June 1999, *J. Kuo & Z. Kanamoto* (CMM). Ishigaki Isl., *T. Ito 1455* (K); W of Shishi Mori, 1.7 km NW of Kabira Peninsula, sandy reef, 1 m, July 4 1956, *F. R. Fosberg 37871* (L61-084598, US2682844, NY); Near mouth of Nagura River, 26 Mar 1981, *R. Yamanishi* (OSA); Nagura Bay, 0.5 m, 14 Nov 1993, *K. Shimamura* (CMM); *loc. cit.*, 2 m, muddy sand, 5 June 1999, *Z. Kanamoto & J. Kuo* (CMM); EN of Todoroki River, 0 m at low tide, on outer edge of inner reef flat, 8 June 1956, *R. Fosberg 3783* (K, US2682841); Fukido River mouth, 1-2 m, sandy mud, 6 June 199, *Z. Kanamoto & J. Kuo* (CMM); Ohama, 4 Nov 1974, *T. Kuwamura* (OSA); Sakieda Bay, 2 m, sand, 6 June 1999, *Z. Kanamoto* (CMM); Tomino Bay, sandy, 6 June 1999, *J. Kuo & Z. Kanamoto* (CMM); Ibaruma Bay 2-3 m, rocky,

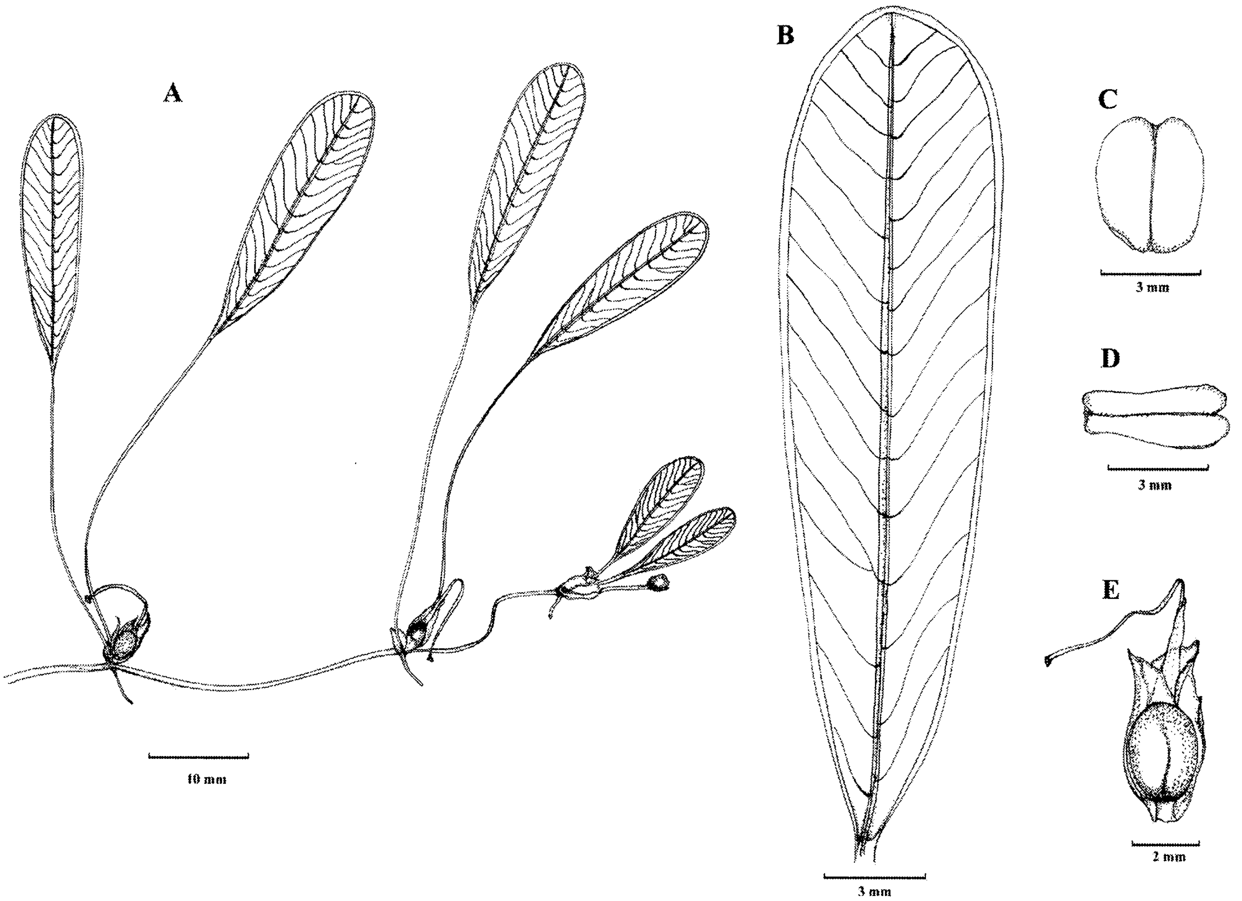

FIG. 5. Drawings of *Halophila mikii* J. Kuo. A, female flowering plant; B, lamina; C, petiole scale (opened); D, rhizome scale (opened); E, maturing fruit with a persisted hypanthium.

sandy bottom, 6 June 1999, *Z. Kanamoto* (CMM). Miyako Isl., Bisseoganzaki, 1 m, 13 Nov 1993, *H. Matsumoto* (CMM); Aragusuku Coast, 1.5 m, 13 Nov 1993, *H. Matsumoto* (CMM); Nagama Coast, 1 m, 13 Nov 1993, *H. Matsumoto* (CMM). Okinawa Isl., Kin Bay, 0.5 m, 30 Dec 1993, *M. Nishihira* (CMM); *loc. cit.*, 1-2 m. with *H. pinifolia, Cymodocea* spp, sandy, 10 June 1999, *Z. Kanamoto* (CMM); Chinen, 1-3 m, with *H. pinifolia*, 9 June 1999, *J. Kuo & Z. Kanamoto* (CMM); Ishikawa Bay, 3-4 m, with *Syringodium, Cymodocea* spp, 10 June 1999, *J. Kuo & Z. Kanamoto* (CMM); Uodomari Is., 31 Oct 1974, *T. Kuwaura* (OSA); Itoman, in sand on coral reef, 10 June 1955, *S. Hatsusima 18133* (TI); *loc. cit.*, Nishizaki, 4-6 m, 5 Mar 1994, *T. Toma* (CMM); Naha City, May 1931, *T. Teramachi* (SAP11062); Yagachi Is., exposed at low tide, June 24 1966, *E. H. Walker 8421* (US2619565); *loc. cit.*, Hanegi Inland Sea, exposed at low tide, 12 June 1999, *J. Kuo & Z. Kanamoto* (CMM); Hirara Bay, 3 m, sandy mud, 30 m^2 patches with *H. pinifolia*, 11 June 1999, *Z. Kanamoto & J. Kuo* (CMM); Heneko, 20 Oct 1999, *S. Tanahara* (private collection). **Kagoshima Pref.**: Yoron Isl., Funakura, 0.5 to 1 m, coral sand, with other tropical seagrasses, 1999, collector unknown (KF). Amami-oshima Isl., southern Amami-oshima, Atetsu, 8 m, white sand; Doren, 3 m, on coral sand, with *Halodule* spp.; Ankyaba, 10 m, on white sand, adjacent to corals, 13 June 1999, *Z. Kanamoto & J. Kuo* (CMM); Maehida, 2-3 m, with *Halodule* spp., 14 June no year, collector unknown (KF); Kasari, 30 Oct 1967, collector unknown (KF); *loc. cit.*, 1-2 m, sandy mud, with *Halodule, Syringodium*, 14 June 1999, *J. Kuo & Z. Kanamoto* (CMM).

Halophila mikii J. Kuo, **sp. nov.** (Figs. 5. 13)
Species *Halophilae nipponicae* J. Kuo affinis sed nervis cruiciformibus 14-17 non 6-10, spatio inter marginem et nervos intra-marginem limitato, et lamina foliorum spathulata nec elliptica satis distincta; a *Halophila ovalis* (R. Br.) Hook. *f*, lamina

foliorum spathulata non ovata nec elliptica bene differt.

Herba marina submersa dioicia; internodia rhizomatis usque ad 55 mm longa, 0.6 mm lata; folia petiolata, petiolo in vivo roseo; lamina viridis, obovata vel spathulata, apice obtusa, basi symmetrica, usque ad 30 mm longa, 7 mm lata, L:W ratio 3 - 4 : 1; nervi utroque costae laterales 14-17; nervi intramarginales ex margine c. 0.1 mm. Floris femineo ovarium ad 1.5 mm longum; hypanthium 8 mm longum. Flores masculini et fructi ignoti.

Typus: JAPAN: **Kagoshima Pref.**: Tanegashima Island, Kumage Gun, Sumiyoshi, 27 Oct 1921, *Z. Tashiro* (KYO).

Dioecious. Perennial. Rhizomes slender, fleshy, transparent; internodes to 55 mm long, 0.6 mm diameter; roots to 35 mm long. Scales 2, glabrous, margins entire, petiole scale 4 × 1.5-2 mm, rhizome scale 4 × 1.2 mm. Leaves petiolate. Petioles fleshy, transparent, 30 mm long. Lamina bright green, obovate to spatulate, to 30 mm long and 7 mm wide, L:W ratio 3 - 4 : 1; apex obtuse; base symmetrically tapped; margin entire; surface glabrous; distance between intramarginal veins and lamina margin 0.2 mm wide; 1/2 lamina width : distance between intramarginal veins and lamina margin ratio ca. 1 : 15; cross veins distinct, 14-17 at each side of the midrib, ca. 60° angles, some branched, distance between adjacent cross veins 1 mm wide. (Female flower) ovary 1.5 mm long; hypanthium 8 mm long. Male flowers and mature fruits unknown.

Distribution and habitats: Halophila mikii is only known from the type locality, Tanegashima Island, and at one locality near the adjacent island, Yakushima Island. No additional material was found in Tanegashima Island during a recent intensive survey (Kuo *et al.* 2006). The species could be a relict. The species grows as patches, 2-5 m^2 from 2-3 m to about 10 m in depth in clear water on gravely sandy mud substratum in sheltered bays. The species was not found to grow with other seagrass species in Yakushima Island, although Miki (1934a) found *Zostera japonica* at the type locality, Tanegashima Island. It is uncertain whether *H. mikii* and *Z. japonica* were previously growing together, as neither species was found at the type locality (Kuo *et al.* 2006).

Biology: Based on the type material, flowering and fruiting may take place from August to October. The material collected from Yakushima Island in June did not contain reproductive material.

Nomenclature notes: Miki (1934a) recognized this *Halophila* from Tanegashima Island as 'Intermediate form' of his three geographic and morphological "forms" of the Japanese *H. ovalis*. Later Miki (1934b) discarded the concept of three 'forms' of *H. ovalis* and recognized only one *Halophila* species, *H. ovalis* in Japan.

Affinity: *Halophila mikii* is similar to *H. ovalis* with wide distributional areas in the Indo-west Pacific regions south of Amami-oshima Island, but can be distinguished from it by the obovate to spathulate lamina of leaves, lamina length : width ratio 3-4, while that of *H. ovalis* is ovate or elliptic, lamina length : width ratio 1.6-2.0. The number of cross veins can also be used to distinguish *H. mikii* with 14-17 from *H. nipponica* with (6-) 7-9 (-10).

Specimens examined: JAPAN: **Kagoshima Pref.**: Kumage Gun, Motoura, Kamiyaku, ca 150 m from the shore, 10 m, sandy mud substrate, 20 June 1994, *T. Matsumoto* (private collection); *loc. cit.*, patches of 2x3 m^2 to 3-5 m^2, 16 June 1999, *Z. Kanamoto & T. Matsumoto* (CMM).

Halophila nipponica J. Kuo, **sp. nov.** (Figs. 6, 13)

A species ex *Halophila mikii* J. Kuo nervis cruiciformibus 6-10 non 14-17, spatio inter marginem et nervos intra-marginem latiore, et lamina foliorum elliptica non spathulata diversa; a *H. majore* crescenti sympatrice in Wakayamensi, Kochiensi et Tokushimensi in Japonia nervis cruciformibus 6-10 non 16-22 satis dignoscenda.

Herba marina submersa dioicia; internodia rhizomatis 15-35 mm longis, 0.8-1.2 mm diam.; folia

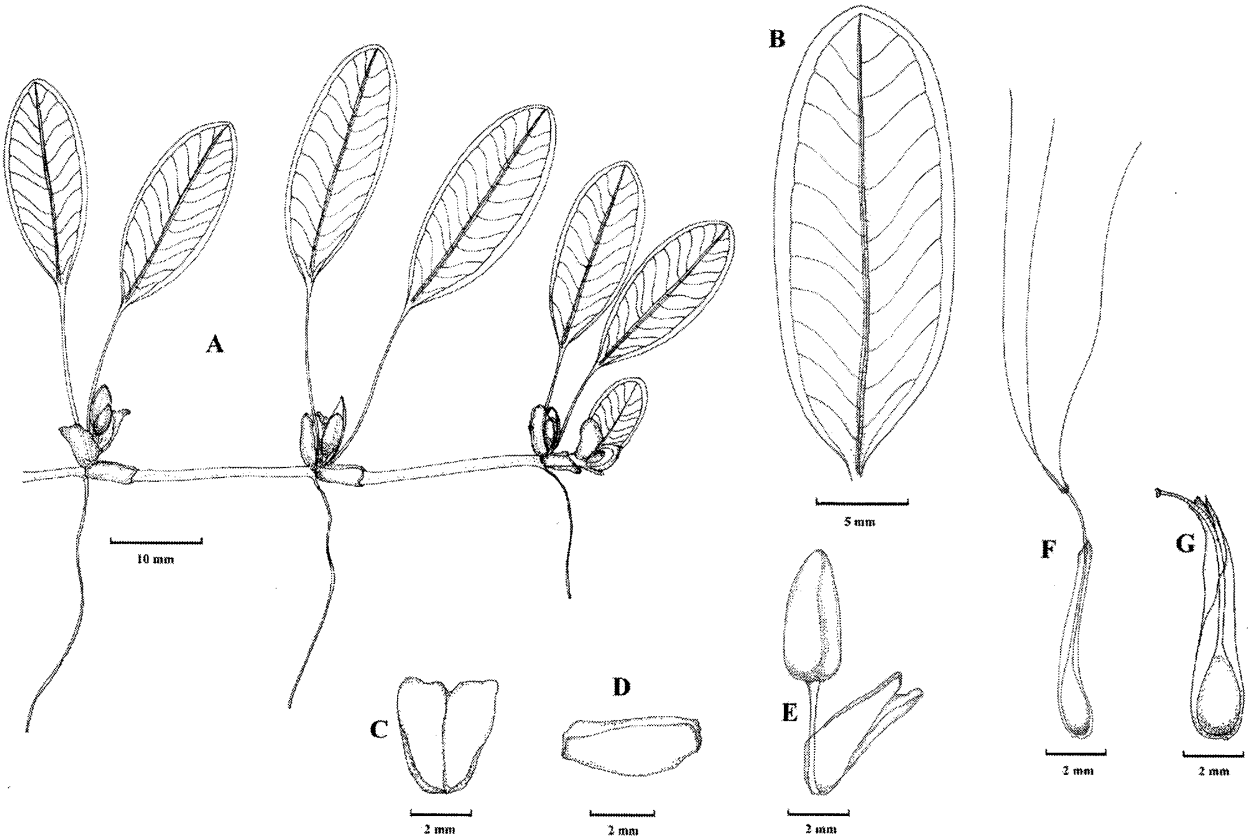

FIG. 6. Drawings of *Halophila nipponica* J. Kuo. A, male flowering plant; B, lamina; C, petiole scale (opened); D, rhizome scale (closed); E, tepals with an extending pedicel; F, female flower with 3 elongated styles; G. female flower with styles detached.

petiolata; petiolus roseus, 5-30 mm longus; lamina viridis, elliptica, apice obtusa vel rotundata, basi cuneata et symmetrica, (12-) 18 - 25 (30) × (3-) 5-9 (-13) mm, L: W ratio (2-) 3 - 4 (-6) : 1, nervi utroque costae laterales integri (6-) 7 - 9 (10); nervus intramarginalis ex margine 0.5-1 mm. Flores masculini: stamina 3-4 × 1.5 mm longa, flava; pedicellus usque ad 6-8 mm longus, antherae oblongae 2.5-3 × 1.5 mm, purpureae. Flores feminei: ovarium 1.5-2 × 1.5 mm; hypanthium 3.5-8 mm longum; stylus 15-25 mm longus. Fructi ovoidei, 3.5-4 × 3-3.5 mm. Semina ovoidea, c. 0.6-0.7 mm, 25-30 in quoque fructu, testa reticulata.

Typus: JAPAN: **Chiba Pref.**: Okinoshima, Teteyama, 12 August 1994, *Y. Hirano* (TNS-holo; TI, MAK, CMM-iso)

Dioecious. Perennial. Rhizomes fleshy, white, internodes 15-35 mm long, 0.8-1.2 mm diameter; roots to 10 cm long. Scales 2, glabrous, margins entire, petiole scale 3.5-4.5 × 1.5-2 mm, rhizome scale 3.5-4 × 1-1.5 mm. Lateral shoots invisible. Leaves petiolate. Petioles fleshy, purple, 5-30 mm long, 0.5-0.8 mm diameter. Lamina bright green, elliptic, (12-) 18-25 (-30) mm long, (3-) 5-9 (-13) mm wide, L: W ratio (2-) 3-4 (-6) : 1; apex apiculate, obtuse to rounded; base cuneate, symmetrical; margin entire; surface glabrous; distance between intramarginal veins and lamina margin 0.5-1 mm wide; 1/2 lamina width : distance between intramarginal veins and lamina margin ratio 1 : 1.5-6.5; cross-veins not distinct, (6-) 7-9 (-10), unbranched, arising at angles of 30°-45°, distance between adjacent cross veins 1.4-2 mm wide. (Male flower) spathal bracts 5 mm long; tepals bright yellow, 3-4 × 1.5 mm; pedicel white, extended to 6-8 mm long, 0.5-0.8 mm thick;

anthers purple, 1.5-2 mm long, 0.2 mm wide. (Female flower) ovary 1.5-2 × 1.5 mm; hypanthium 3.5-8 mm long; styles 15-25 mm long; persisting hypanthium 3.5-8 mm long. Fruit ovoid, covered by keeled yellowish to brownish spathes, 3.5-4 × 3-3.5 mm. Seeds 25-30, ovoid, ca 0.6 × 0.7 mm, bluntly beaked at both ends; testa reticulate.

Distribution and habitats: *Halophila nipponica* is endemic to Japan and is only distributed in temperate regions from Kagoshima Bay along the west coast of Kyushu and the west coast of Honshu (including the Oki Islands) to Matsu Bay in Aomori Prefecture in the Sea of Japan. The species also occurs in the Seto Inland Sea, Kochi and Tokushima Prefectures in Shikoku, and from Kii Peninsula in Wakayama Prefecture to Tokyo Bay in the western Pacific Ocean. The species grows as isolated small patches or with temperate *Halophila major* or *Zostera marina* and *Z. japonica*, even with *Z. caespitosa* Miki, in sheltered bays from 2 to 15 m on muddy and/or sandy sediment.

Biology: Both male and female flowers have been collected from August to September.

Nomenclature notes: When Makino (1912) described the new species *Halophila euphlebia*, he also illustrated H. ovalis without description (see Bot. Mag. Tokyo 26: 209, Fig. XVI). This illustration appears to belong to *H. nipponica*. As stated previously, this new Japanese taxon has been treated as *H. ovalis* (Makino 1912, Miki 1934b, den Hartog 1970).

Affinity and morphological variation: *Halophila nipponica* exhibits some morphological variations depending on the localities. Populations from Misaki area, Chiba Pref. always bear larger plants with a large blade (12-) 15-23 (-28) × (4.5-) 7-9 (-13) mm, with L:W (2.5) 3-4: 1; those from Noto Peninsula have a slender lamina (17-) 20-25 (30) × (3-) 4 - 6 (-8) mm, with L:W ratio 3-5 (-6): 1; and plants from Kyushu have a broader lamina (14-) 18 × (6-) 8-10 mm, L:W ratio 2.0-2.2 (-2.5): 1. Regardless of these differences in lamina size, all populations maintain their unique morphological characters with (6-) 7-9 (-10) unbranched cross veins and a wide distance between the intramarginal veins and lamina margin. These unique characters of *H. nipponica* can be easily used to distinguish this species from the temperate *H. major*, as they occur sympatrically in Wakayama, Kochi and Tokushima Prefectures, or to separate this species from other related subtropical Japanese *Halophila* species such as *H. ovalis* and *H. minor*.

Selected specimens examined: JAPAN: **Kagoshima Pref.**: Kagoshima, Kamoike, 2-3 m, muddy bottom, 21 June 1999, *J. Kuo & Z. Kanamoto* (CMM); Sakurajima, Fukuyama, 3-5 m, muddy, patches of 2-3 m diameter, 21 June 1999, *J. Kuo & Z. Kanamoto* (CMM); Kagoshima, Chosa, Matsubara, 29 July 1915, *T. Tashiro* (KYO); Kagoshima, Taichi, 15 Aug 1910, *Z. Tashro* (TNS19766); Shibushi, Natu, 2 May 1988, *K. Minagata* (KYU). **Nagasaki Pref.**: Nishisonogi gun, Kikitsu mura, 28 Oct 1906, *T. Tashiro* (TNS30181, KYO); Tomioka Wan, *J. Kuo & S. Nojima* (CMM). **Ehime Pref.**: Off Nakajima Marine Biological Station, 6 m, 7 Mar 1990, 4-9.5 m, 24 July1994, 24 July, 28 Aug, 9 Sept 1998, *Z. Kanamoto* (CMM). **Kagawa Pref.**: Takamatsu City, no other information (MAK226964). **Kochi Pref.**: Toyo Cho, Kannoura, 6-7 m, with *Z. japonica* and *H. major*, 9 June 1998, *Z. Kanamoto* (CMM). **Tokushima Pref.**: Narutoshi, 11 Sept 1965, *K. Abe* (TNS162594, 174931). **Yamaguchi Pref.**: Umashima, Tabuse Town, Maruyama Kaigan, 3-4 m, muddy sand, adjacent to *Zostera japonica/Z. marina* meadows, 26 June 1999, *J. Kuo & Z. Kanamoto* (CMM). **Shimane Pref.**: Himane, Oki Island, 16 Aug 1916, collector unknown (TI); Hishi, 10 Aug 1922, *Y. Ikoma* (OSA); Kamo Bay, 2-6 m, with *Z. marina/Z. caespitose*, 30 June 1999, *J. Kuo & Z. Kanamoto* (CMM). **Hiroshima Pref.**: Takahara Shi, 1911, *J. Shiragami* (MAK226963). **Osaka Pref.**: Osaka, Tanigawa, Misaki Cho, Sennan Gun, 5 m, sandy bottom, 21 Aug 1980, *R. Yamanishi* (OSA34275, 34276). **Wakayama Pref.**: Tanabe, Shirahara, Aug 1902, *K. Minagata* (MAK196340); Tanabe Bay, 26 Sept 1924, *K. Matsushima* (TNS37494); Tanabe Bay, Hatakejima, with *H. major*, 1924, *T. Makino* (MAK226960); Off Seto MBS, 0.5 to 1 m, with *H. major*, 21-23 Sept 1993, *T. Kato* (CMM). **Shizuoka Pref.**: exact locality unknown, 10 Aug 1914, *R. Endo* (TUS34098); Izu, Nakagi, 8-10 m, sand bottom, 20 Aug and 12-13 Sept 1993, *M. Aoki & A. Dasai* (CMM). **Kanagawa Pref.**: Miura gun, Aboratsubo Bay, dragged, 19 July

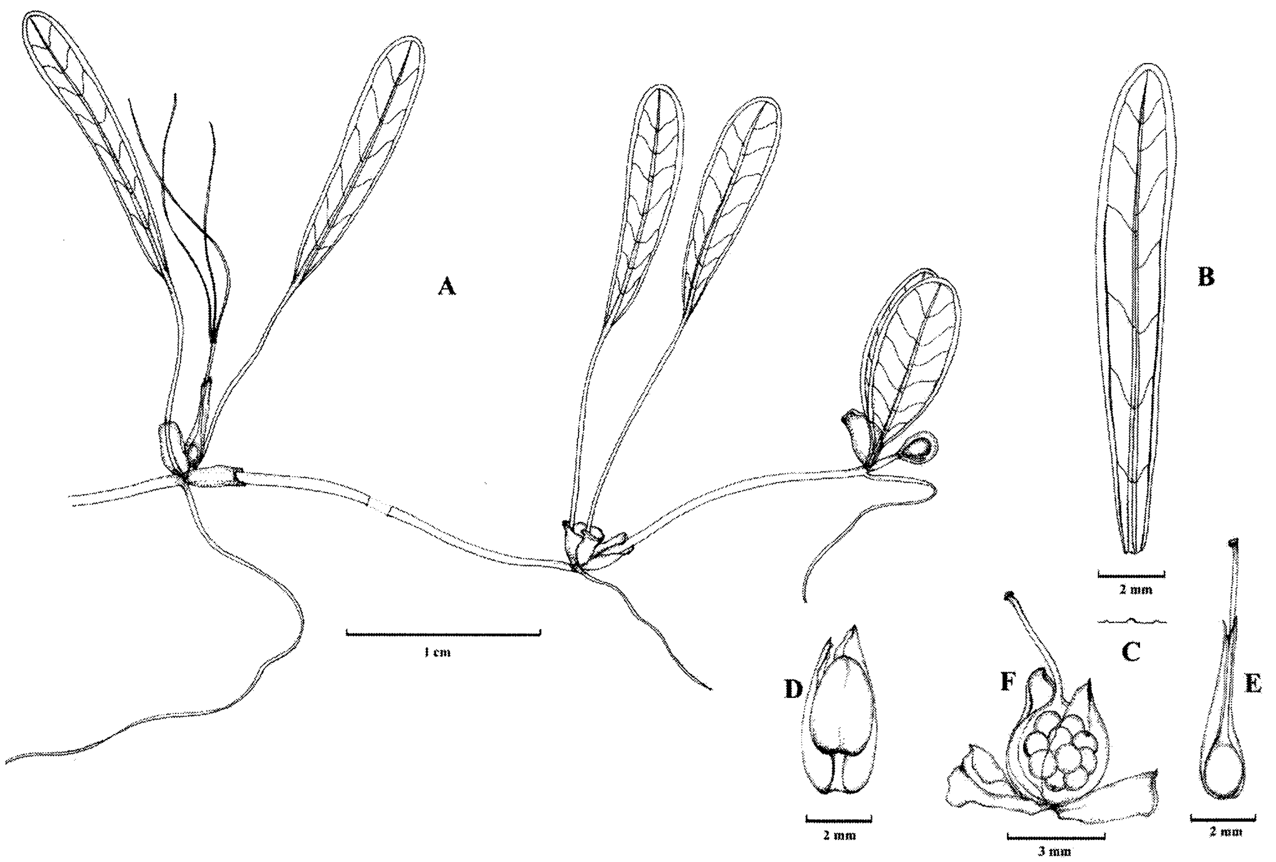

FIG. 7. Drawings of *Halophila okinawensis* J. Kuo. A, female flowering plant; B, lamina; C, side view of the abaxial surface of lamina showing protuberances of the midrib (center) and intramarginal veins (peripherals); D, tepals with a slightly extending pedicel; E, female flower (post anthesis) without styles; F, maturing fruit.

1899, *Y. Yabe* (TI); 20 Aug 1900, *H. Toku* (SAP); Aug 1909, *J. Nakai* (TI); 21 Aug 1919, *S. Miki* (OSA); 15 Aug 1958, *K. Arai* (TNS137635); Misaki coast, 31 May 1931, *Y. Komori* (TI); Misaki, Aboratsubo, 30 May 1951, *I. Hurusama* (9 sheets, TI). **Chiba Pref.**: Boshu-Funakata, 29 Mar 1952, *S. Asano* (TNS97533). Okinoshima, Teteyama, 14 Aug 1926, *Y. Ikoma 4* (OSA), *loc. cit.*, 10 June, 12 July, 12 Aug, 6 Sept 1994, *Y. Hirano* (CMM). **Kyoto Pref.**: Maizuru Bay, shallow sea, no date, *H. Tanaka* (MAK226961); Wakasa Bay, Ine Aoshima, May 1996, *Douke/Itani* (CMM). **Ishikawa Pref.**: Noto, Nanao shi, Nanao wan, Gousaki, 3 Aug 1910, *H. Ichimura* (TI), *loc. cit.*, Sept 1988, *O. Sano* (CMM); Suzu gun, Uchiura cho, Ogi, 27 Aug 1962, *N. Satomi* (KYO, TNS15238), *loc. cit.*, 22 June 1988, *H. Iizumi* (CMM); Tsukumo Bay, 19 Aug 1927, *Y. Ikoma* (OSA), *loc. cit.*, near Noto Marine Biological Station, 1-4 m, 2, 3, 11, 21, 31 Aug, 10 Sept 1990, *O. Sano* (CMM); 3 m, with *Zostera marina*, 13 July 1998, *Z. Kanamoto* (CMM); *loc. cit.*, 6 July 1999, *J. Kuo & Z. Kanamoto* (CMM). Matsushima, Kinoumuira, 6 July 1999, *J. Kuo & Z. Kanamoto* (CMM). **Aomori Pref.**: Mutsu Bay, Yomogida, 9.7 m, 22 July 2004, *S. Kirihara* (CMM).

Halophila okinawensis J. Kuo, **sp. nov.** (Figs. 7, 14)

Halophila minori (Zoll.) den Hartog, affinis, sed lamina lineari vel spathulata basi angustata et spatio inter marginem et nervos intra-marginem latiore et nervis cruciformibus non ramificantilus differt.

Herba marina submersa dioicia; internodia rhizomatis usque ad 35 mm longa, 0.2-0.3 mm diam.; folia petiolata, petiolo albido, 5-15 mm longo; lamina flavovirenti, ventraliter parum curvata, anguste elliptica vel obovata, 12-16 mm longa, 1.5-4.5 mm lata, L:W ratio (2.5-) 3.5 - 4 (-7), apice rotundata, basi asymmetrica, margine integra, nervis integris

(3-) 4 - 6 (-7) in quoque latere costae. Flores masculini stamine 2.5-3 mm longo; pedicellus ad 20 mm longus; anthera 2.5-3 mm longa, 0.5 mm lata. Flores feminei ovario 1.5 × 0.5 mm; hypanthium 4-6 mm longus; stylus ad 30 mm longus. Semina c. 15 in quoque fructu, ovoidea, c. 0.5 mm diam., testa reticulata.

Typus: JAPAN: **Okinawa Pref.**: Okinawa Isl., ca. 100 m from causeway, southern Kin Bay, 8-9 m, 22 May 1997, *Z. Kanamoto* (TNS-holo; TI, MAK, CMM-iso)

Dioecious. Rhizome internodes thin, to 35 mm long, 0.2-0.3 mm diameter. Scales 2, glabrous, margins entire, rhizome scale 2.5-3 × 0.5 mm, petiole scale 3-3.5 × 1 mm. Lateral shoots invisible. Leaves petiolate. Petioles whitish, 5-15 mm long. Lamina yellow green, distinctly linear to spatulate or narrowly elliptic; slightly abaxially curved inwards; 12-16 mm long, 1.5-4.5 mm wide, L:W ratio (2.5-) 3.5-4 (-7); apex rounded; base asymmetrically narrowed; margin entire; surface glabrous; distance between intramarginal veins and lamina margin 0.25-0.3 mm wide; 1/2 lamina width: distance between intramarginal vein and lamina margin ratio ca. 1 : 2-9.5; midrib and intramarginal veins distinct, with protrusions; cross veins indistinct, (5-) 6-7, unbranched; distance between adjacent cross veins ca. 2 mm wide. Spathal bracts 3-5.5 mm long, lanceolate, acute. (Male flower) Spathal bracts 3-5.5 mm long; tepals 2.5-3 mm long, 1.5-2.5 mm wide; pedicel to 20 mm long and 0.45 mm wide at anthesis; anthers 2.5-3 mm long. (Female flower) ovary ellipsoid to ovoid, white, 1.5 mm long, 0.5 mm wide; hypanthium 4-6 mm long; style to 30 mm long. Seeds ca. 15, ovoid, 0.5 mm diameter; testa reticulate.

Distribution and habitats: *Halophila okinawensis* has been collected from several localities including Kin Bay, Nakagusuku Bay, Awase and Sesoko Island in Okinawa Island. The species grows in clear water between 15 to 24 m deep on sand, muddy sand and coral sand substratum in Okinawa Island and at 20 to 30 m in Iriomote Island. It grows as mono-specific sparse patches or with *H. decipiens* and *H. gaudichaudii.*

Biology: The flowers (both pre and post anthesis) of *Halophila okinawensis* have been collected in late May. It is anticipated that fruits of this species mature in July-August.

Nomenclature notes: Tsuda & Kamura (1990) may have seen this taxon collected from Sesoko Island and commented, "this taxon seems to be closest to *Halophila ovalis* ssp. *linearis* (Hartog) Hartog (1970)". *Halophila ovalis* ssp. *linearis* bears lamina 17-25 mm long and 1.5 mm wide with about 10 cross veins and comes from Mozambique, Eastern Africa (den Hartog 1970; Kuo & den Hartog 2001), while *H. okinawensis* has lamina 12-16 mm long, 1.5-4.5 mm wide with less than 7 cross veins.

Affinity: This new species can be easily distinguished from *Halophila minor*, by having a distinctly linear to spatulate lamina with a wider lamina marginal space and un-branched cross veins.

Specimens examined: JAPAN: **Okinawa Pref.**: Okinawa Isl., Kin Bay, 15 m, 26 Dec 1993, *M. Nishihira* (CMM), *loc. cit.*, 13 m, 22 Apr 1996, *Z. Kanamoto* (CMM); *loc. cit.*, 6.5 m, 25 June 1997, *Z. Kanamoto* (CMM); *loc. cit.*, 4-7.5 m, with *Halodule pinifolia*, 5 Oct 1998, *Z. Kanamoto* (CMM); Nakagusuku Bay, off Ikeijima light-house (GPS E26-23-606; N27-59-439), 17 m, 4 May 2001, *S. Tanahara* (private collection); Awase, with *H. decipiens*, 6 m, 9 May 2003, *S. Arai* (CMM); *loc. cit.*, 5.5 m, mud substratum, with *H. decipiens, H. uninervis, Thalassia hemprichii*, 15 June 2003, *S. Tanahara* (private collection); Nishizaki, 6-7 m, 5 Mar 1994, *T. Toma* (CMM); Sesoko Island, 24 m, sandy substratum, with *H. decipiens*, 26 Aug 1994, *N. Nishihira* (CMM).

Halophila gaudichaudii J. Kuo, **sp. nov.** (Figs. 8, 15)

A species ex *Halophila minori* (Zoll.) den Hartog affinis sed nervis cruiciformibus (3-) 4-8 non 7-12, spatio inter marginem et nervos intra-marginem latiore.

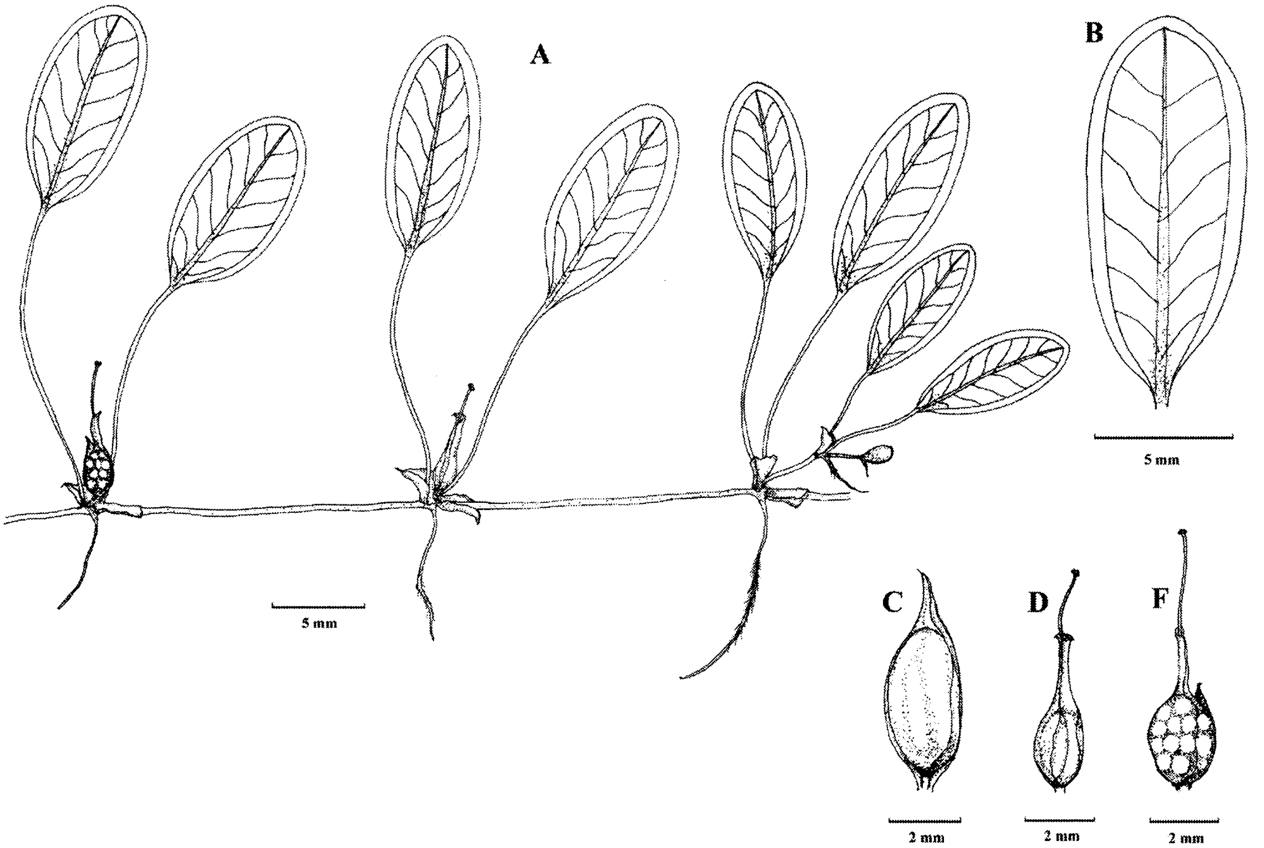

FIG. 8. Drawings of *Halophila gaudichaudii* J. Kuo. A, female flowering plant; B, lamina; C, tepals; D, female flower with styles already detached (post anthesis); E, maturing fruit.

Herba marina submersa dioecia; internodia rhizomatis 10-30 mm longa, 0.4-0.8 mm diam; folia petiolata, petiolo 10-15 mm longo; lamina obovata, apice rotundata, basi cuneata, symmetrica, (-8) 10-15 (-17) × (3.5-) 4-6 (-8) mm, L:W ratione (1.6) 2-2.4 (-2.6) : 1; nervi laterales 4-8 utroque costae latere, integri; spatio intervenium 1-1.75 mm; nervus intramarginalis ex margine 0.4-0.6 mm; ratio laminae latitudinis et spatio inter venas intramarginalis et marginem laminae 5-6.7. Flores masculini: bracteae spathales 2.5-3.5 × 1.5 mm; stamina 3.5-4 mm longa; pedicellus 4-10 mm longus; antherae 1.5-3 × 1-1.2 mm. Flores feminei: bracteae spathales 4-5 mm longae; ovarium 1.5 mm longum; hypanthium 3-6 mm longum; stylus 6-20 mm longus. Fructi ovoidei 2-4 × 1.5-3 mm. Semina ovoidea c. 0.5 mm, 6-30 in quoque fructu; testa reticulata.

Typus: Marianna Island: sine loc. exact, *C. Gaudichaud* (P-holo; K-drawings of the type)

Dioecious. Perennial. Rhizome internodes 10-30 mm long, 0.4-0.8 mm diameter. Lateral shoots invisible. Scales 2, glabrous, margins entire, rhizome scale 3 × 0.5-1 mm, petiole scale 3 × 1-1.5 mm. Leaves petiolate. Petioles whitish, 10-15 mm long. Lamina bright green, obovate, (8-) 10-15 (-17) mm long, (3.5-) 4-6 (-8) mm wide, L: W ratio (1.6-) 2-2.4 (-2.6); apex rounded; base rounded; margin entire; surface glabrous; distance between intramarginal veins and lamina margin 0.4-0.6 mm wide; 1/2 lamina width : distance between intramarginal vein and lamina margin ratio ca. 1 : 4.0-8.3; cross vein (3-) 4-8, arising at angles of 30°-45°, unbranched, distance between adjacent cross veins 1.75 mm wide. (Male flower) spathal bracts 2.5-3.5

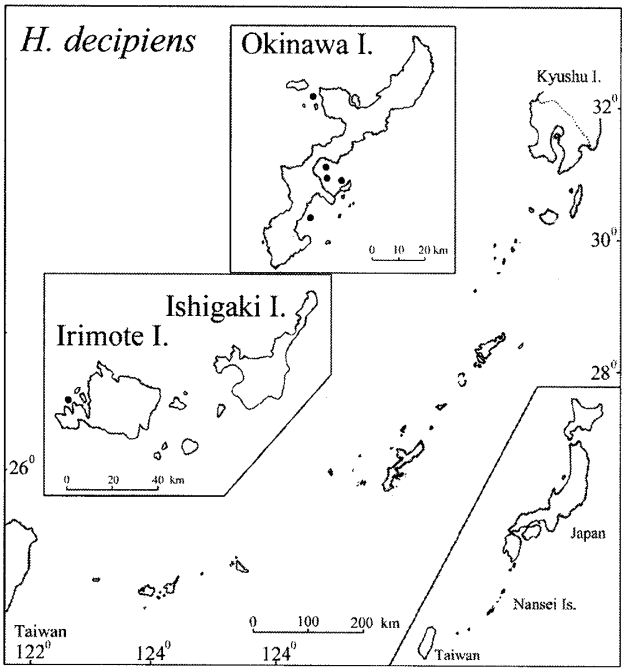

FIG. 9. Distribution of *Halophila decipiens* in Japanese waters.

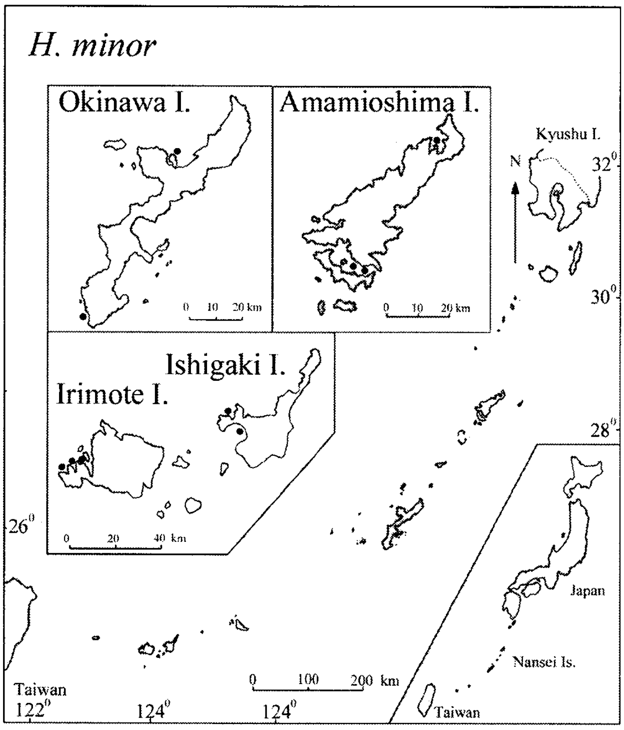

FIG. 10. Distribution of *Halophila minor* in Japanese waters.

× 1.5 mm; stamens 3.5-4 mm long; pedicel 4-10 mm long; anthers 1.5-3 × 1-1.2 mm. (Female flower) spathal bracts 4-5 mm long; ovary ellipsoid to ovoid, white, 1.5 mm long, 1 mm wide; hypanthium 3-6 mm long; style 6-20 mm long. Fruits ovoid, 2-4 × 1.5-3 mm. Seeds ca. 6-30, ovoid, ca 0.5 mm diameter; testa reticulate.

Distribution and habitats: This species is widely distributed in tropical regions of the western Pacific Ocean but only occurs in a few localities in Okinawa Island in Japan. It grows with *Halophila ovalis*, *H. minor* and *H. pinifolia* at shallow water (5-7 m) or with *H. decipiens* and *H. okinawensis* in deeper water (24 m).

Biology: The flowers of *Halophila gaudichaudii* have been collected in late May at Okinawa Island. Flowering and fruiting material have been collected from Guam, Saipan, New Caledonia and Manila Bay in the Philippines from January to April.

Nomenclature notes: Gaudichaud (1826, 1829) described the *Halophila* specimen from Marinas Islands as *Halophila ovata*, but the name of *H. ovata* was based on *Caulinia ovalis* R. Brown (see Gaudichaud 1826, p. 65; 1829, p. 429-430). In 1827, he also illustrated *H. ovata*, without referring to *C. ovalis*, as Fig 40 in his publication. If the dates of publication of the relevant parts of Gaudichaud's *Voyage Uranie*, as cited by Sachet & Fosberg (1973), are correct (and these correspond to those given by Stafleu and Cowan in TL2) then *H. ovata* Gaud. must be treated as an illegitimate synonym of *H. ovalis* (R. Br.) Hook. *f.* On p. 65, Gaudichaud (1826) states that (translated): "also a singular phanerogam described under the name *C. ovalis*, R. Brown. *Prod.* p. 339, but which according to M. Aubert du Petit-Thouars (Gen. nov. Madagasc. p. 2) is of the genus *Halophila*. I have drawn it, plate 39 (actually 40), fig. 1." This definitely indicates that Gaudichaud considered that *C. ovalis* and *H. ovata* were the same species, a synonymy he repeats on p. 430 (1829) where he cites *C. ovalis* as a synonym of *H. ovata*. Joseph Hooker (1858), in Fl. Tasm., in making the new combination under *Halophila* "corrects" Gaudichaud's spelling of the epithet to

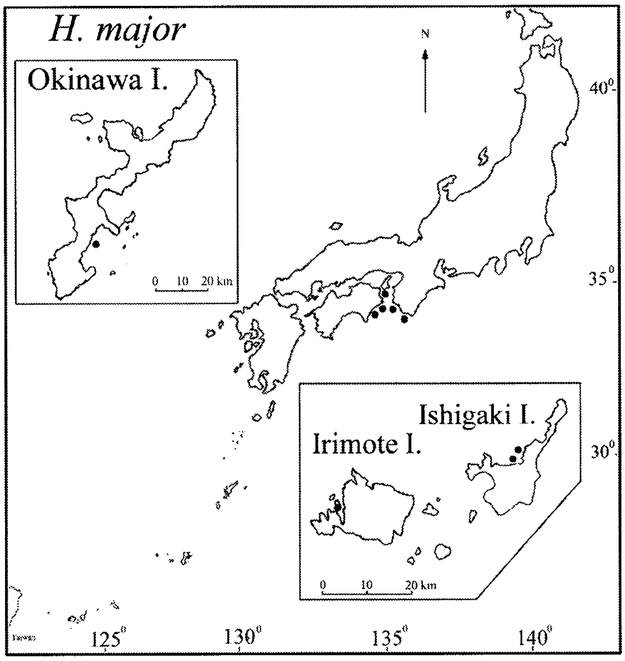

FIG. 11. Distribution of *Halophila minor* in Japanese waters.

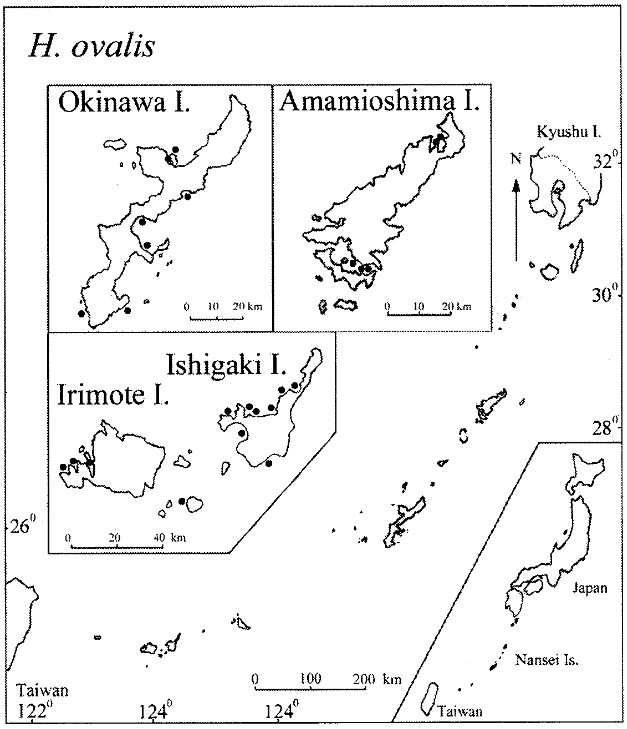

FIG. 12. Distribution of *Halophila ovalis* in Japanese waters.

"*ovalis*"; presumably he thought that Gaudichaud had accidentally misspelt the name. Ascherson (1868) recognized *H. ovata* as one of three varieties of *H. ovalis*, but in his subsequent publications he did not mention this species, presumably because he considered it to be *H. ovalis*. Ostenfeld (1909), based on material from the type locality, the Marianne Island and from the Philippines, reconfirmed that *H. ovata* differs from *H. ovalis*. Den Hartog (1957), probably based on Fig. 40 of Gaudichaud (1827), which did not list as a synonym of *C. ovalis*, considered that *H. ovata* was a synonym of *H. minor*, however, he later (1970) reversed the order and made *H. minor* a synonym of *H. ovata*, which he recognized had priority. Sachet & Fosberg (1973) pointed out that the name of *H. ovata* has nomenclature illegitimacy as it was based on *C. ovalis* (as stated above). These authors further discussed at great length *H. ovata* versus *H. minor* and concluded that these two 'names' are the same species and listed *H. ovata* as the synonym of *H. minor*. Kuo (2000) demonstrated that *H. ovata* and *H. minor* are two different species, but did not provide a new name to replace *H. ovata*. Thus, the incorrect name of *H. ovata* has been continuously used until now (Kuo & den Hartog 2001, Green & Short 2003, den Hartog & Kuo 2006).

Affinity: Because the size of this species is very similar to that of *Halophila minor*, they have been considered to be the same species, and placed either under the name of *H. minor* or *H. ovata* (now as *H. gaudichaudii*) (see den Hartog 1957, 1970, Sachet & Fosberg 1973). However, the space between lamina margin and intramarginal veins, the space between adjacent cross veins and the number of cross veins all clearly demonstrate that *H. gaudichaudii* and *H. minor* are two distinct species (see also Kuo 2000).

Selected specimens examined: JAPAN: **Okinawa Pref.**: Okinawa Isl., Kin Bay, 15 m, 26 Dec 1993, *M. Nishihara* (CMM); *loc. cit.*, 13 m, 22 Apr 1996, *Z. Kanamoto* (CMM); *loc. cit.*, 6.5 m, 25 June 1997, *Z. Kanamoto* (CMM); *loc. cit.*, 4-7.5 m, with *Halodule pinifolia*, 5 Oct 1998, *Z. Kanamoto* (CMM); Nakagusuku Bay, off Ikei jima light-house (GPS E26-23-606; N27-59-439), 17 m, 4 May 2001, *S. Tanahara* (private collection); Awase, with *H. decipiens*, 6 m, 9 May 2003, *S. Arai* (CMM); *loc. cit.*, 5.5 m, mud substratum, with *H. decip-*

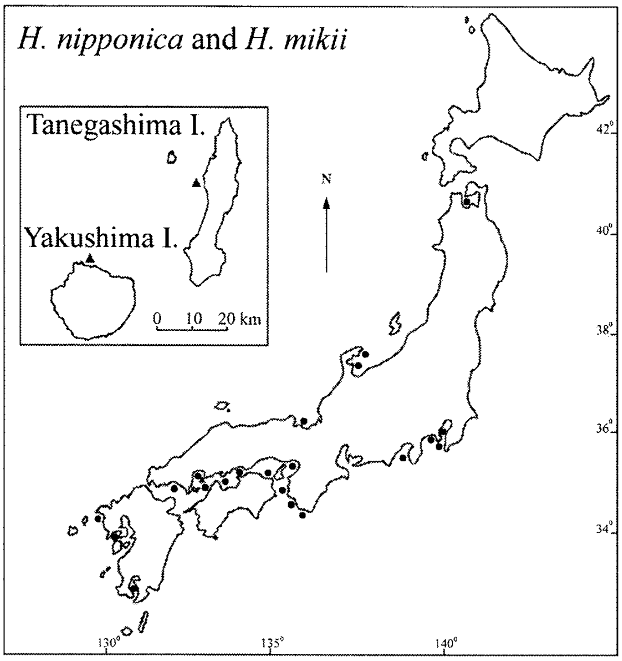

FIG. 13. Distribution of *Halophila H. mikii* (triangles) and *H. nipponica* (solid circles) in Japanese waters.

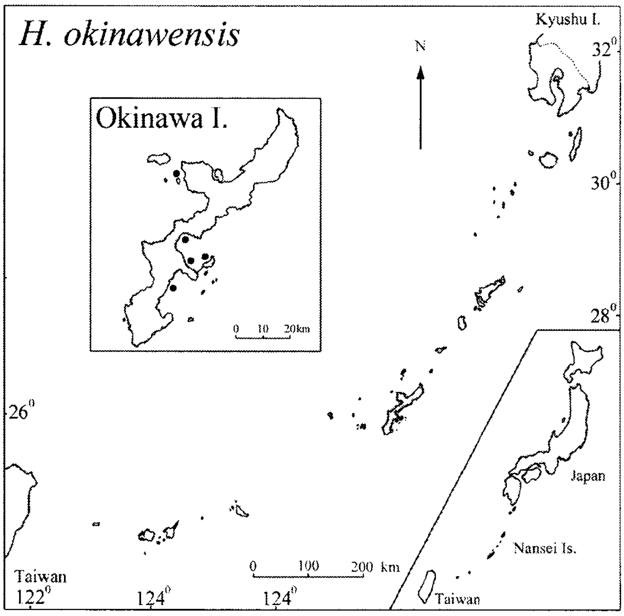

FIG. 14. Distribution of *Halophila okinawensis* in Japanese waters.

iens, *H. uninervis*, *Thalassia hemprichii*, 15 June 2003, *S. Tanahara* (private collection); Itoman, Nishizaki, 6-7 m, 5 Mar 1994, *T. Toma* (CMM); Sesoko Island, 24 m, sandy substratum, with *H. decipiens*, 26 Aug 1994, *M. Nishihira* (CMM).

Discussion

This taxonomic study reveals that eight *Halophila* species belonging to Section *Halophila* are present in Japanese waters instead of only one or two species (Maekawa *et al.* 1988, Kitamura *et al.* 1998, Aioi & Nakaoka 2003) or six species (Uchimura *et al.* 2005) as previously reported. Differences in the species number are mainly due to the fact that no critical taxonomic study on the Japanese *Halophila* has been carried out until now. Most plants of Section *Halophila* are rather small and morphologically simple (Kuo & den Hartog 2006); only few vegetative morphological characters, including the shape and size of lamina, lamina length and width ratio, the number of cross veins, and the distance between the intramarginal veins and lamina margin, can be used for accurate species identification (Kuo & den Hartog 2001). In addition, reproductive characters are insufficient for recognizing these species. Therefore, based on reproductive characters alone, one can superficially combine all Japanese *Halophila* species, with an exception of *H. decipiens*, and consider them as a 'collective' species or conspecific species with *H. ovalis* as had been proposed by den Hartog (1970) and Green & Short (2003) respectively. All these species have ovate to elliptic and even to spatulate lamina with branched or unbranched cross veins of 3 to 22 on each side of the midrib. However, a detailed analysis of the above-mentioned morphological characters in Japanese *Halophila* specimens has revealed that eight distinctive taxa can be recognized as described above. Beside morphological features, most of species have their own distributional ranges and habitat preferences. A preliminary work conducted by Uchimura *et al.* (2005) has supported the present study by reporting up to six species of *Halophila* existing in Japan, although they did not have an opportunity to analyse the material of all taxa mentioned in this study, for example, *H. mikii* is currently only known from one remote locality at

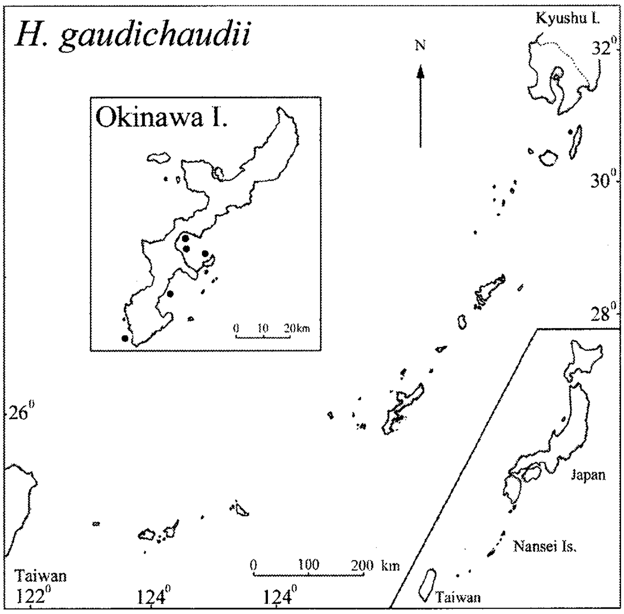

FIG. 15. Distribution of *Halophila gaudichaudii* in Japanese waters.

Yakushima Island. Furthermore, they have misidentified some Japanese species such as the entity they call *H. australis*, which in fact, is a species endemic to temperate Australia (Kuo & den Hartog 2001).

Halophila decipiens is the deepest seagrass occurring in Japan; it has been collected at 38 m in Amino Bay, Iriomote Island (Kuo *et al.* 2006) as in the Philippines (Meñez & Calumpong 1985). In contrast, the same species occurs at a range of 2 to 40 m on sand and mud substrata in southern Taiwan (Mok *et al.* 1993). Furthermore, *H. decipiens* is considered as an annual species in Japanese waters (Kuo *et al.* 1995). The annual populations of *H. decipiens* have also been recorded in shallow waters from Panama (McMillan & Soong 1983) and from south-western Australia (Kuo & Kirkman 1995).

The Japanese *Halophila major*, *H. ovalis* and *H. minor* sometimes co-exist in the intertidal or shallow waters of subtropical Japan, however, rhizomes of these plants produce their species-specific lamina sizes with distinct numbers of cross veins. Therefore, it is essential to count cross vein numbers besides measuring lamina size for more accurate identification of Japanese *Halophila* species. It is very possible that the previously reported *H. ovalis* from the Ryukyu Islands (*e.g.*, Tsuda & Kamura 1990, Toma 1999) may represent three different species: *H. ovalis*, *H. major* and *H. minor*. Both *H. okinawensis* and *H. gaudichaudii* may coexist with *H. decipiens* in the deeper waters off Okinawa Island, but these species can be easily distinguished using the characters of lamina morphology and the number of cross veins as described above. *Halophila okinawensis* has distinctly linear to spatulate lamina with cross vein numbers of (5-) 6-7; while *H. gaudichaudii* has an obovate lamina with cross vein numbers of (3-) 4-8. *Halophila nipponica* is morphologically closest to *H.hawaiiana*, which is restricted to the Hawaiian Archipelago and Midway Island (McDermid *et al.* 2003). Both species have fewer unbranched cross veins in comparison to typical *H. ovalis*. However, *H. nipponica* is easily distinguished from *H. hawaiiana* by having a wider space between intramarginal vein and lamina margin. As in the case of *H. hawaiiana* (McDermid *et al.* 2003), *H. nipponica* also displays a distinct leaf morphological form at different localities in temperate Japan, but all have a constant number (6-) 7-9 (-10) of cross veins. From the present study it can be suggested that the previously recorded *H. ovalis* from Kyushu (Noro & Nanba 1989) and most parts of Honshu Islands (*e.g.*, Sano *et al.* 1978, 1981, Fugita & Takayama 1999, Kitahara *et al.* 2005) represent *H. nipponica*, while those records from Shikoku (Tanada *et al.* 2005) and Wakayama Prefecture may contain both *H. major* and *H. nipponica*.

It is interesting to note that the Japanese *Halophila major* has two populations with disjunct geographic distributions, which are separated for more than 1000 km. The temperate adapted population (which had been identified as *H. euphlebia*) is restricted to Shikoku and Wakayama Prefectures in Honshu, while the tropic-adapted population is extended from the tropical West Pacific and Indian Oceans. Furthermore, *H. mikii* can be considered as relict species due to the fact that only female plants have been observed with a very restricted distribution. *Halophila nipponica* is widely distributed in temperate Japanese waters but is not present in Hokkaido Island, which indicates that the species is a temperate but not a cold adapted species. This species occurs principally in warmer temperate regions along the west coast of Japan from Kagoshima Bay to Mutsu Bay and seems to be influenced by the warm Tsushima Current. On the other hand, this species extends only from southern Honshu to Chiba Peninsula and is absent in northeastern Honshu on the east coast, suggesting that the winter Oyashio Current may prevent the species extending beyond Tokyo Bay. However, a report of sighting this species (as *H. ovalis*) at Mano Bay, Sado Island by Honma & Kitami (1978) is yet to be confirmed. Furthermore, the occurrence at Mutsu Bay (41°N, 140°40'E) makes *H. nipponica* the most northerly distributed temperate species in the genus *Halophila* (see also Kitahara *et al.* 2005).

The Japanese *Halophila* species, with an exception of *H. major*, clearly have distinct subtropical and temperate distributions. It is interesting to note that only one of the six subtropical *Halophila* species (*H. okinawensis*) but both temperate species (*H. nipponica* and *H. mikii*) are endemic to Japanese waters. Most subtropical Japanese *Halophila* species have clearly spread from the tropical Indo-Pacific region due to the influences of the warm Kuroshio Current (Miki 1934b; Mukai 1993). Islands in the Nansei Archipelago serve as the northern distributional boundary for several tropical *Halophila* species, that is, Okinawa Island for *H. decipiens* and *H. gaudichaudii*, and Amami-oshima Island for *H. ovalis* and *H. minor* (Kuo *et al.* 2006).

Currently, up to twenty-two seagrass species can be found in Japanese waters including eight *Halophila* species from the present study. The Japanese seagrass species clearly have distinct subtropical and temperate distributions, with the exception of *Zostera japonica* and *H. major*, which occur in both areas. All thirteen Japanese subtropical seagrasses, with the exception of *H. okinawensis*, have obviously under the influence of the warm Kuroshio Current to spread from the tropical region to their northern distributional limits in southern Japan. In contrast, temperate/cold adapted Japanese seagrasses, including two *Phyllospadix* species and five *Zostera* species, also occur in other areas in the North West Pacific and five of these seven species are endemic to this region. The temperate adapted *Halophila* species are confined to Japanese waters and do not extend to other north east Asian countries, such as Korea, Russia and temperate China. The rich diversity of endemic seagrass species in the temperate Northwest Pacific including temperate Japan is comparable to that in temperate Australia where eighteen out of twenty-two species are endemic. Thus, these two temperate regions have the most diverse seagrass species in the world but the reasons for this diversity require further investigation.

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References

Aioi, K. & M. Nakaoka. 2003. The seagrasses of Japan. *In*: Green, E. P. & F. T. Short. (eds.) World Atlas of Seagrasses, pp. 185-192. Univ. California Press, Berkeley.

Ascherson, P. 1868. Vorarbeiten zu einer Uebersicht der phanerogamen Meergewächse. Linnaea 35: 152-208.

——. 1882. Order CXX. Hydrocharitaceae. *In*: Boissier, P. E. (ed.) Fl. Orient Flora Oreintalis. Plantae Vasculaqres. Class. II. Monocotyledoneae. 5: 1-26.

——. 1888. Die Geographische Verbreitung der Seegräser. *In*: von Neumayer, G. (ed.) Anl. wiss. Boeb. Reisen, 2nd ed., pp. 191-212.

——. 1906. Die geographische Verbreitung der Seegraser. *In*: von Neumayer, G. (ed.) Anl. Wiss. Boeb. Reisen, 3rd ed., 2: 389-413.

Brown, R. 1810. Prodromus Florae Novae Holaniae et Insulae Van-Diemen. Taylor, London.

——. 1960 (Fascimie ed.). Prodromus Florae Novae Holaniae et Insulae Van-Diemen (1810), Supplementum primum (1830) by Robert Brown with an introduction by William T. Stearn. Hafner, New York.

Den Hartog, C. 1957. Hydrocharitaceae. *In*: van Steenis, C. G. G. J. (ed.) Fl. Malesia. II. ser. I, 5: 381-413.

——. 1970. Sea-grasses in the World. North-Holland, Amsterdam.

—— & J. Kuo. 2006. Seagrass taxonomy and biogeography. *In*: Larkum, A. W. D., R. T. Orth & C. M. Duarte. (eds.) Seagrasses: Biology, Ecology and Conservation, pp. 1-23. Springer, Amsterdam.

Doty, M. S. & B. C. Stone. 1966. Two new species of *Halophila* (Hydrocharitaceae). Brittonia 18: 303-306.

—— & ——. 1967. Typification for the generic name *Halophila* Thouars. Taxon 16: 414-418.

Fugita, D. & S. Takayama. 1999. Records of sea grasses *Halophila ovalis* and *Zostera japonica* off Uozu City, Toyama Prefecture. Bull. Toyama Pref. Fishery Res. Inst. 11: 67-70. (in Japanese with English abstract)

Gaudichaud, C. 1826, 1827, 1829. 'Voyage autour du monde, par Louis de Freycinet.' Botanique.

Green, E. P. & F. T. Short. (eds.) 2003. World Atlas of Seagrasses. Univ. California Press, Berkeley.

Honma, Y. & T. Kitami. 1978. Fauna and flora in the waters adjacent to the Sado Marine Biological Station, Niigata University, Ann. Rep. Sado Mar. Biol. Sta, Niigata Univ. 8: 7-81. (in Japanese)

Hooker, J. D. 1858. The botany of the Antarctic voyage of H. M. Discovery Ships *Erebus* and *Terror*, in the years 1839-1843, under command of Captain Sir James Clark Ross. III. Flora Tasmaniae. Volume 2 (Monocotyledones). Reeve, London.

Ito, T. 1899. Some remarkable marine monocotyledons in Japan. Ann. Bot. 13: 464-465.

Kitahara, S., D. Fugita & M. Notoya. 2005. Records of seagrass *Halophila ovalis* in Mutsu Bay, Aomori Prefecture, Japan. SOURUI (Jap. J. Phycol. 53: 237-239). (in Japanese with English abstract)

Kitamura, S., G. Murata & T. Koyama. 1998. Coloured Illustrations of Herbaceous Plants of Japan (3rd ed.), Vol. III (Monocotyledoneae). Hoikusha, Osaka. (in Japanese)

Kuo, J. 2000. Taxonomic notes on *Halophila minor* and *Halophila ovata*. Biol. Mar. Medit. 7: 79-82.

—— & C. den Hartog. 2001. Species identification. *In*: F. T. Short, F. T. & R. G. Coles. (eds.) Seagrass Global Research Methods, pp. 31-58. Elsevier, Amsterdam.

—— & ——. 2006. Seagrass morphology, anatomy and ultrastructure. *In*: Larkum, A. W. D., R. T. Orth & C. M. Duarte. (eds.) Seagrasses: Biology, Ecology and Conservation, pp. 53-88, Springers, Amsterdam.

——, Z. Kanamoto, T. Toma & M. Nishihira. 1995. Occurrence of *Halophila decipiens* Ostenfeld (Hydrocharitaceae) in Okinawa Island, Japan. Aquat. Bot. 51: 329-334.

——, ——, H. Iizumi, K. Aioi & H. Mukai. 2006. Seagrasses from the Nansei Islands, southern Japanese Archipelago: Species compositions, distribution and biogeography. J. Marine Ecol. (in press).

—— & H. Kirkman. 1995. *Halophila decipiens* Ostenfeld in estuaries of southwestern Australia. Aquat. Bot. 51: 335-340.

——, T. Shibuno, Z. Kanamoto & T. Noro. 2001. *Halophila ovalis* (Br.) Hook. from a submarine hot spring in Southern Japan. Aquat. Bot. 70: 329-335.

Maekawa, F., H. Hara & T. Tuyama. 1988. Makino's New Illustrated Flora of Japan. Hokuryukan, Tokyo. (in Japanese)

Makino, T. 1896. (Marine angiosperms found in the sea surrounding Japan. In a miscellaneous note on rocky shore, no. 27). Bot. Mag. Tokyo (115): 313-322. (in Japanese)

——. 1912. Observations on the flora of Japan. Bot. Mag. Tokyo 26: 208-210.

——. 1961. Makino's New Illustrated Flora of Japan. Hokuryukan, Tokyo. (in Japanese)

Matsumura, J. 1895. (Miscellaneous notes on Botany). Bot. Mag. Tokyo 9: 67-70. (in Japanese)

——. 1905. Hydrocharitaceae. Index Plantarum Japonicarum. Vol. 2. pp. 31-33. Maruze, Tokyo. (in Japanese)

McDermid, K. J., M. C. Gregoritza, J. W. Reeves & D. W. Freshwater. 2003. Morphological and genetic variation in the endemic seagrass *Halophila hawaiiana* (Hydrocharitaceae) in the Hawaiian Archipelago. Pac. Sci. 57: 199-209.

McMillan, C. & K. Soong. 1989. An annual cycle of flowering, fruiting and seed reserve for *Halophila decipiens* Ostenfeld (Hydrocharitaceae) in Panama. Aquat. Bot. 34: 375-379.

Meñez, E. G. & H. P. Calumpong. 1985. *Halophila decipiens*, an unreported seagrass from the Philippines. Proc. Biol. Soc. Wash. 98: 232-236.

Miki, S. 1934a. On the sea-grasses in Japan (II). Cymodoceaceae and marine Hydrocharitaceae. Bot. Mag. Tokyo 48: 131-142.

——. 1934b. On the Sea-Grasses in Japan (III). General consideration on the Japanese sea-grasses. Bot. Mag. Tokyo 48: 171-178.

Miquel, F. A. W. 1855. Flora van Nederlandsch Indie drede Deel. Fried. Fleischer, 3: 229-230.

Mok, H,-K., J.-D. Lee & C.-P. Lee. 1994. A new record of seagrass, *Halophila decipiens* Ostenfeld (Hydrocharitaceae) in Taiwan. Bot. Bull. Acad. Sin. 34: 353-356.

Mukai, H. 1993. Biogeography of the tropical seagrasses in the Western Pacific. Aust. J. Mar. Freshwater Res. 44: 1-17.

Noro, T. & S. Nanba. 1989, Distribution and seasonality of seaweeds in Sakurajima Is., Kagoshima, Japan. Mem. Fish. Kagoshima Univ. 38: 69-76. (in Japanese)

Ohwi, J. & M. Kitagawa. 1983. New Flora of Japan. Shibundo, Tokyo. (in Japanese)

Ostenfeld, C. H. 1902. Hydrocharitaceae, Lemnaceae, Pontederiaceae, Potamogetonaceae, Gentianaceae (Limnanthemum), Nymphaceae. Bot. Tidsskr. 24: 260-263.

——. 1909. On *Halophila ovata* Gaudichaud, a neglected species. Philip. J. Sci. 4: 67-68.

Phillips, R. C. & E. R. Meñez. 1988. Seagrasses. Smithsonian Contributions to the Marine Sciences. Number 34. Smithsonian Institution, Washington, D. C.

Robertson, E. L. 1984. Seagrasses. *In*: Womersley, H. B. S. (ed.) The marine benthic flora of Southern Australia. Part I, pp. 57-122, Government Printer, Adelaide.

Sachet, M.-H. & F. R. Fosberg. 1973. Remarks on *Halophila* (Hydrocharitaceae). Taxon 22: 439-443.

Sano, O., M. Ikemori & M. Arasaki. 1978 Distribution and ecology of *Acetabularia calyculus* and *Halophlya* (sic) *ovalis* the coast of Toyama Bay in Noto Peninsula. J. Geo. Bot. 26: 49-61.

——, —— & ——. 1981. Distribution and ecology of *Acetabularia calyculus* along the coast of Noto Peninsula. Jap. J. Phycol. 29: 31-38.

Tanada, N., S. Arai & T. Terawaki. 2005. Habitats of seagrass *Halophila* on the coast of Tokushima Prefecture. Bull. Tokushima Pref. Fish. Res. Ins. 4: 23-28. (in Japanese with English abstract)

Tanaka, N. 2005. Typification of Dr. Makino's botanical names (1). J. Jap. Bot. 80: 22-26.

Thouars, L. M. A. Du Petit. 1806. Genera nova Madagascariensia secundum methodum Jussiaeanam disposita. Paris.

Toma, T. 1999. Seagrasses from the Ryukyu Islands. I. Species and distribution. Biol. Mag. Okinawa 37: 75-92. (in Japanese with English abstract)

Tsuda, R. T. & S. Kamura. 1990. Comparative review on the floristics, phytogeography, seasonal aspects and assemblage patterns of the seagrass flora in Micronesia and the Ryukyu Islands. Galaxea 9: 77-93.

Uchimura, M., S. Arai, T. Miyazaki, N. Yokoyama, T. Inoue, Y. Nakamura & S. Shimada. 2005. (New findings on the taxonomy of *Halophila* in Japan). Jap. J. Phycol. 53: 98. (An abstract for the 29th Annual Meeting of the Japanese Society of Phycology, Kyoto, Japan, 28 March 2005.) (in Japanese)

*——. E. J. Faye, S. Shimada, S. Arai, T. Inoue & Y. Nakamura. 2006. A re-evaluation of the taxonomic status of *Halophila euphlebia* Makino (Hydrocharitaceae) based on morphological features and ITS sequence data. Bot. Mar. 49: 111-121.

Yamashita, T. 1991. Hydrocharitaceae. *In*: Satake, Y., J.

Ohwi, S. Kitamura, S. Watari & T. Tominari. (eds.) Wild Flowers of Japan. Herbaceous Plants (including dwarf shrubs), pp. 3-7. Heibonsha, Tokyo. (in Japanese)

Waycott, M., D. W. Freshwater, R. A. York, A. Calladine & W. J. Kenworthy. 2002. Evolutionary trends in the seagrass genus *Halophila* (Thouars): insights from molecular phylogeny. Bull. Mar. Sci. 70: 1299-1308.

Zollinger, H.1884. Sysrematisches Verzeichniss der im indischen Hrelolpdf in den Jahren 1842-1848 gesammelten sowie der aus Japan empfangenen Pflanzen. 1: 71-75.

* Based on morphological characters and ITS molecular data sequence studies, Uchimura *et al.* (2006) concluded that *Halophila major* (under the name of *H. euphlebia*) in Japanese waters is a distinct taxon.

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